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SPATIAL AND TEMPORAL PATTERNS OF BAT ACTIVITY IN A SOUTHEAST NEBRASKA AGRICULTURAL LANDSCAPE

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by

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Intensive agriculture is associated with biodiversity loss and species decline. Yet wild species, such as bats, may provide critical ecosystem services to agriculture, even in transformed landscapes. In the United States, bats have been estimated to save the agricultural industry billions of dollars per year. However, white-nose syndrome and habitat loss have led to the decline of many bat species in North America, including the federally threatened northern long-eared bat, *Myotis septentrionalis*.

To better evaluate the effectiveness of these pest-controlling services, and to increase understanding of bat foraging behavior in these extreme landscapes, I deployed 11 grids of 24 detectors, in 6 x 4 formation, 100 m apart in crop fields bordering different edge habitats, sampling each once over a period of four nights. Bat activity was highest at sites with the most wooded edge habitat, and sites with more trees and water typically had the most species diversity. While bat activity and species richness were low at isolated habitat fragments and sites with minimal habitat edges, overall insect availability remained abundant in fields as by field edges, suggesting less hunting pressure on insect pests in these areas. I found high degrees of species temporal overlap and failed to detect any significant negative spatial or temporal relationships between species.

I also conducted capture and tracking surveys for threatened northern long-eared bats at Homestead National Monument of America to document roosting behavior at the western edge of this species range. I tracked two individuals to rooting sites, each bat using multiple structures, one selecting trees and snags two miles upstream of the park, and another using tree cavities and shadowbox fences in the park with other untagged northern long-eared bats. These results suggest that wooded areas, riparian zones, and human-built structures are important resources for this imperiled species, especially in intensively managed agricultural landscapes. Since these environments are likely to increase across the globe, more research is needed to better understand how bat species interact with one another and the landscape to allow for their persistence in these extreme ecosystems.

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CHAPTER 1: SPATIAL DISTRIBUTION OF BAT ACTIVITY IN AGRICULTURAL FIELDS

Abstract

Intensive agriculture has many negative effects on biodiversity, and it is important to understand how wildlife species exploit available habitats to allow persistence in these human-modified landscapes. Bats provide a number of ecosystem services in agricultural areas, including the predation of night-flying insects, for which they are estimated to save agricultural industries billions of dollars per year. To better evaluate the effectiveness of these pest-controlling services, and to increase understanding of bat foraging behavior in these extreme landscapes, I used a novel acoustic grid sampling approach to document spatiotemporal activity patterns by different bat species along various crop field edges in southeast Nebraska. I sampled each plot once over a period of four nights. Bat activity was highest at areas with the most wooded edge habitat, and sites with more trees and water typically had the most species diversity. While bat activity and species richness were low at isolated habitat fragments and sites with minimal habitat edges, overall insect availability remained abundant in fields as by field edges, suggesting less predation pressure in open crop fields. Woodland interfaces are important habitat for bats, however woody invasions can alter ecological structure in fire-sensitive grasslands and lead to a loss of ecosystem services. Consequently, species-level habitat differences and scales of habitat associations are important to consider when formulating systems-level resource management strategies.

Introduction

Agriculture is one of the primary drivers of global change, with crop yield expansion rate outpacing that even of human population growth, resulting in the destruction of natural ecosystems and increased fertilizer and pesticide use (Matson et al., 1997; Tilman et al., 2001; Tscharntke et al., 2005; Meehan et al., 2011). In many regions, crops are planted in large monocultures to maximize production and profit, causing ecosystem simplification, and leading to species decline and the loss of ecosystem services provided by wildlife (Tilman et al., 2001; Daily & Ehrlich, 2001; Tscharntke et al., 2012; De Beenhouwer et al., 2013).

As the primary predator of night flying insects, bats are thought to play a major role in consuming insect pests (Cleveland et al., 2006; Boyles et al., 2011; Maine & Boyles 2015) and serve as bio-indicators of ecosystem health (Park, 2015). In rural landscapes, areas of forest cover are important habitat for bats, especially tree-roosting as well as narrow and edge-space foraging species (Estrada & Coates-estrada, 2001; Harvey et al., 2006; Henderson & Broders, 2008; Wolcot & Volunec, 2012). Isolated trees, riparian zones, and water bodies have also been indicated as important habitat for these flying mammals (Lumsden & Bennett, 2005; Harvey & Villalobos, 2007; Fuentes-Montemayor et al, 2013; Kalda et al., 2014), even in grassland habitats (Holloway & Barclay, 2000; Heim et al., 2015; Treitler et al., 2016). Bats will also navigate using vegetation structures as location references and guides while flying (Jensen, 2005). Hedgerows, windbreaks, and other linear features are common in many agricultural landscapes, and are utilized by many foraging bats (Walsh & Harris, 1996; Frey-

Ehrenbold et al., 2013; Kelm et al., 2014). Forests and streams can additionally serve as travel corridors (Estrada & Coates-Estrada, 2002).

However, not all bat species respond similarly to landscape modification associated with agriculture. Some species forage more intensively over agricultural fields (Heim et al., 2016) than in available native habitat (Williams-Guillén & Perfecto, 2011; Noer et al., 2012; Heim et al., 2016). Generalist species have been documented foraging in a variety of habitats (Estrada & Coates-Estrada, 2002), while more specialized species seem less common in fragmented, intensively farmed areas, suggesting an unwillingness or inability to move through the various agriculture habitat types (Walsh & Harris, 1996; Estrada & Coates-estrada, 2001; Harvey & Villalobos, 2007; Freudmann et al., 2015). Agricultural intensification has also been shown to have minimal influence on species richness in some regions (Williams-Guillén & Perfecto 2011; Treitler et al., 2016; Mtsetfwa et al., 2018), in contrast to other findings (Freudmann et al. 2015) documenting negative affects on forest specialists (Henderson & Broders, 2008; Cleary et al., 2016; Heim et al., 2016; Mtsetfwa et al. 2018).

In agricultural landscapes, bats likely play important roles in insect pest control and suppression, and attempts have been made to quantify these services. (Kunz et al., 2011; Maine & Boyles, 2015). Cleveland et al. (2006) investigated Brazilian free-tailed bat and cotton bollworm behavioral interactions across cotton plantations in 8 southwest Texas counties, estimating the bats pest control services at roughly $74/acre. Boyles (2011) applied these ecosystem service estimates to the cropland acreage of the continental United States, arriving at an approximate value range of U.S. $3.7 to $53 billion/year. Maine and Boyles (2015) also extrapolated their findings from a few corn

fields in Illinois to global corn savings of approximately U.S. $1 billion/year. However, simply scaling up results from one or a few species in a handful of study sites fails to account for habitat requirements, geographic ranges, and foraging behaviors of the different bat species that actually occupy the areas extrapolated to. This strategy also neglects the crucial concept of scale with which species interact with their environment (Peterson et al., 1998; Hein et al., 2006; Treitler et al., 2016).

The purpose of this study was to examine the spatial activity patterns of bat species in intensively managed agricultural fields in the midwestern United States using a novel acoustic sampling method. Determining how bat species utilize the current agricultural matrix is critical in quantifying their roles in pest suppression, identifying habitat needs for conservation, and gaining a better understanding of bat foraging behavior in these landscapes. My objectives were to: 1) determine if bat species forage homogenously over crop fields or are limited to certain habitat features and 2) determine if insect abundance is higher along field edge habitats than in crop fields. I hypothesized that bat activity would be different for each species and not homogenous, but rather concentrated by areas with woody vegetation and water, and little activity in open crop fields, and that insect biomass would decline away from edges. The spatial extents of bat foraging distributions over time through this unique sampling method presents a different way to view bat movements, and offers a deeper insight into bat ecology, with considerable implications for the ecosystem services they provide.

Methods

Study Area

I conducted this study on privately managed crop fields in Gage and Lancaster Counties, located in southeast Nebraska. I selected study areas using ArcMap (10.7.1), each encompassing an area of 400 meters by 600 meters of corn and/or soy, as well as one restored native tallgrass prairie site. Located in the North American Great Plains region, Nebraska was historically a prairie ecosystem dominated landscape prior to European settlement. The region is now heavily managed for the production of corn and soybean, and is characterized by large tracts of open farmland on flat, upland plains, interspersed with riparian buffers, windbreaks, and patches of mature lowland forest.

Detector Setup and Site Selection

I selected crop fields that were at least partially bordered by some form of tree cover or other natural habitat feature. I also included two sites with no immediate habitat edge to gather additional information on activity over expansive crop fields. Agricultural sites were privately owned and managed by different landowners for the production of corn and/or soybean, while the restored prairie plot was maintained by the National Park Service. I used AnaBat Express passive zero cross acoustic detectors (Titley Scientific, Brendale, QLD, Australia, www.titleyscientific.com) to record bat activity. Since each Express unit has a maximum optimal range of 50 meters, I used ArcGIS to create a layer of points each 100 meters apart to form a transect grid that bordered the habitat feature and extended into the open crop field, spanning a detection area 400 meters by 600 meters that employed 24 detectors (Mtsetfwa et al., 2018). I then entered the coordinates

for these locations into hand-held Garmin GPSMAP 64 units for actual detector placement in the field.

I mounted each detector on a modified painter's pole extended 4 meters above the ground so all units cleared any crop cover for increased recording quality (Mtsetfwa et al., 2018). I positioned detectors such that every detector's omnidirectional microphone faced into the open and away from tree clutter. I left detectors at each deployment site for 4 consecutive nights, with each detector set to begin recording from at least 30 minutes before sunset until 30 minutes after sunrise. If there was sustained heavy rain, low temperatures, or high winds during a deployment session, I left detectors out for additional nights as needed, until 4 sampling nights with optimal weather conditions were obtained. Issues with battery life occurred on two sites, so I redeployed problem detectors and a combination of different nights were used in both cases, using as many identical nights as possible across detectors. Sampling took place from June through August.

Acoustic Analysis

I downloaded and ran raw acoustic detector files through AnalookW software (Titley Scientific) (Mancina et al., 2012; Fuentes-Montemayor et al, 2013) to convert files to individual "bat passes" for further analysis. I analyzed all recordings using Kaleidoscope v5.1.9 with the Bats of North America 5.1.0 classifier set to "+1 More Accurate" (Wildlife Acoustics, Concord, MA, USA; www.wildlifeacoustics.com). I used Kaleidoscope's recommended default signal parameters as follows: 8-120kHz frequency range, 2-500ms length of detected pulses, 500ms inter-syllable gap, 2ms minimum number of pulses, and activated the advanced signal processing feature. Under the Bats

of North America 5.1.0 classifier, the selected species included in the identification process were: big brown bat (*Eptesicus fuscus*), eastern red bat (*Lasiurus borealis*), hoary bat (*Lasiurus cinereus*), silver-haired bat (*Lasionycteris noctivagans*), little brown myotis (*Myotis lucifugus*), northern myotis (*Myotis septentrionalis*), evening bat (*Nycticeius humeralis*), and tricolored bat (*Perimyotis subflavus*). Kaleidoscope Pro looks for unique characteristics in the acoustic calls that makes the identification process of calls to species more feasible, and also outputs the presence probability of a particular species (Willcox et al., 2017). By summing up the numbers of identified acoustic "bat pass" files, an index of bat species activity was obtained by location and time.

Interpolation Maps

I analyzed all identification output results from Kaleidoscope Pro in R (3.6.2, R Core Development Team). Additionally, I created spatial interpolation maps for each site using the ArcMap (10.7.1) kriging tool method, which relies on spatial autocorrelation to assist in determining where species concentrated their activities among sites. Species call counts were matched to each detector point making up the grid shapefile, and these were used to create bins and an interpolated surface map layer. Since bat data were not normally distributed, I used simple kriging with normal score transformation, which transforms the data to standard normal distribution. I also performed a sensitivity test between several transformation methods, including log, box-cox, none, and normal score, and found no significant differences in the mapping results.

Insect Analysis

To gain insight into insect prey distribution, six of the eleven plots were used to collect insects at increasing distances from tree cover. I collected insects with 22W

fluorescent black light traps (Black Light Trap 2851M, BioQuip Products, Rancho Dominguez, California) using three traps for each sampling session, placed at 20m, 220m, and 420m from the field edge. Insect sampling occurred only after the acoustic component had taken place and detectors were removed. I suspended each light trap just above crop canopy by running a rope cord through the trap top handle and tied to extendable painter's poles on either side of the trap, which could be adjusted as needed for the trap light to clear the crop canopy. I turned on traps within 45 minutes of sunset and collected after 5 hours. I emptied light trap contents into freezer Ziploc bags for freezer storage, and upon analysis, allowed approximately 24 hours to thaw. To estimate volume, I transferred insects from each trap separately to 250 mL graduated cylinders and settled by tapping prior to the measurement of volume (Allen et al., 2001). This provides an index of insect biomass at different distances from field edges to determine if insect biomass decays with distance from tree cover.

Statistical Analysis

I conducted all analyses in R (3.6.2, R Core Development Team). For analysis, I pooled data from 4 nights at each site, since activity has been found to vary even on a nightly basis relative to variables including temperature, prey, weather, and moon phase (Kunz, 1973; Hayes, 1997; Ciechanowski et al., 2008; Barros et al., 2014; Heim et al., 2017). For kriging results, I classified contours using equal intervals, with the number of classes relative to the number of calls for each species. Bins for highly active bats were in roughly 20 call increments, with higher bins averaging an additional 5 bat passes per night for a "significant" activity level increase. Less active species however, especially those with little spatial autocorrelation, I often grouped in just enough classes to show

differences in the interpolated surface. I did not create maps for species at sites with low call counts or no spatial autocorrelation, which kriging could not support.

I conducted regression analyses to examine the effects of distance from areas of significant tree cover on species activity levels. I matched species calls to detectors, and grouped these based on relative distances to the nearest significant source of tree cover, ignoring single, isolated trees. Linear regression models were then conducted for species with sufficient data for each site. For sites where detector grids were not bordered directly by any significant landscape feature (site 6, 10 Fig.1.1), distances were measured to the nearest source of tree cover in ArcMap (10.7.1), which in most cases were small shelterbelts around isolated homesteads.

Results

Bat Presence

Total bat activity was highest at sites with the most tree cover and water availability, and lowest at sites with little to no edge habitat (Table 1.1). At any given site up to 8 bat species were detected. Hoary bats (11,842 calls) and big brown bats (10,888 calls) were the most frequently detected, while evening (7,259 calls), eastern red (6,105 calls), and silver-haired (1,466) were also recorded at all sites. Additionally, northern long-eared bats (159 calls) and little brown (153 calls) were active on a few sites where larger forest fragments and tree cover were present (Table 1.2, Fig.1.1). Tricolored bats (131 calls) were similar to both *Myotis* species with activity on forested sites, but in one instance were also detected over a corn field with virtually no tree cover (Table 1.2). Big browns were most active at sites with water present, as were eastern red, hoary, silver-haired, and evening bats. However, big brown, eastern red, hoary, and

evening bats were also regularly present in areas of little tree cover as well, which suggests that these species venture out into open habitats (Table 1.2, Fig. 1.2-1.8).

Interpolation Maps

Maps for sites 1, 2, 3, 4, 5, 7, and 11 (Fig. 1.2-1.8) revealed overall bat activity to be highly concentrated along woody edges and over small water bodies with a rapid decline into open crop fields. Sites with minimal landscape features surrounding the sampled fields tended to have little to no spatial autocorrelation across samples and species. In these instances, the semivariogram kriging model consisted of a very shallow or flat line, and interpolation maps were not applicable. This often occurred among species at sites with little edge habitat, where bats were not drawn to any particular feature, and where overall bat activity was also very low. As a result, bat activity was not mapped for sites 6, 8, 9, and 10.

Big brown bats were primarily active along woodland edges (sites 1 and 5), as well as over water bodies (sites 2, 4, and 7). Isolated trees and windbreaks were also utilized (sites 3 and 7); however overall activity levels were very low at these outlying habitat features. Minimal big brown activity was documented over crop fields across all sites.

Eastern red bats concentrated their activity over creeks and forest edge habitats, respectively, with high fidelity to water bodies (sites 2, 4, and 7), and a rapid decline into surrounding crop fields (sites 4, 5, 7, and 11). These bats were most active species along the riparian woodland (site 1), however, there was no spatial autocorrelation in the dataset. Eastern red bats were also widely distributed over crop fields in one instance (site 2) and also used isolated tree features (sites 3 and 7), as did the big brown bats.

Hoary bats were present at all sampling sessions, but activity was only spatially correlated at half the crop sites. No spatial correlation occurred at sites with little to no edge habitat for this species. Although primarily active along wooded edges across all sites, as well as creeks and ponds, this species was still often detected beyond 200 meters into crop fields, despite rapid declines from edge habitat.

Evening bats were also primarily active along the field edges and over water bodies (sites 1, 2, 4, 5, 7 and 11). Very low activity and spatial correlation existed in acoustic data for this species at sites with little to no edge habitat. Evening bats additionally utilized isolated tree features (sites 3 and 7), but with very little activity above crop field areas.

Silver-haired bats were detected at all sampling areas, however call totals only exceeded 100 total passes at four sites (Table 1.2), and observable spatial patterns were only found at a few sites. In these cases, this species was almost exclusively detected by the forest edges and creeks (sites 1, 4 and 5). Low spatial autocorrelation also occurred at sites with water and forest present (sites 7 and 11) despite relatively high detection rates by tree cover.

Little brown, northern long-eared, and tricolored bats were detected primarily at sites with high amounts of tree cover. These species were the most infrequently detected across sites and were only detected along forest edges and small ponds, often with very little spatial autocorrelation (sites 3, 5, 7, and 11). Northern long-eared bats were primarily detected in the riparian woodland at site 1, the only site that contained detectors within forested habitat, and were not documented beyond the forest edge.

Linear Regression

Most bat activity was negatively correlated with respect to distance from tree cover (Table 1.3, Fig. 1.9-1.19), except for northern long-eared bats, which were not related to distance to any features. However, most relationships between species activity levels and distance from tree cover were not statistically significant (Table 1.4). All species were most active within 200 meters of edge habitats.

Insect Sampling

Of the six sites sampled with insect light traps, insect volume at three sites appeared to increase with respect to distance from tree cover (Table 1.5, Fig. 1.10). Habitat features at sites 3 and 5, which consisted of single windbreaks bordered by soybean fields, also had the highest insect volume totals of all the sampled sites. Site 11 was the only non-crop plot, consisting of a restored tallgrass prairie, and had the second lowest total measured insect volume of the six sites. The other three crop sites appeared to have overall decreasing insect abundance with increasing distance from habitat edges (Table 1.5), and consisted of a creek, riparian corridor, and a buffer strip, respectively.

Discussion

This is the first study to assess spatiotemporal habitat use by bats in an agricultural landscape utilizing acoustic grids, enabling the visualization of landscape use by bats. Acoustic results indicated that forested areas, edge habitats, and patches of tree cover are important areas for bats in a typical Great Plains agricultural landscape. However, the seemingly lack of bat activity over crop field airspace, where insect abundance persists, has considerable implications for the ecosystem services bats may

actually provide, as opposed to the economic values projected by prior small scale extrapolative studies.

Across all sites, bats tended to be most active along forested areas and edges, with fairly rapid decay rates into open arable fields. Habitat edge type also seemed to influence the number of species present and the amount of total bat activity. At the six most utilized sites, water was present in the form of creeks or ponds (Table 1.1, Fig. 1.1), and those with forest patches also contained the highest number of species (Table 1.2). Bats have been found to use these features as travel corridors for traveling through agricultural areas (Verboom & Spoelstra, 1999; Estrada & Coates-Estrada, 2002) and waterbodies for foraging (Walsh and Harris, 1996; Davidai et al., 2015; Heim et al., 2017).

Although bat activity was highest along forested areas, a few bat species were still present at even the most isolated features sampled, including tree patches, single trees, windbreaks, and open field detectors 800 meters away from woody vegetation. This behavior demonstrates that even remote and small scale resources are important refuges for wildlife, even in large scale agriculturally converted landscapes. Other studies have similarly found bats foraging by scattered and isolated trees (Lumsden & Bennett, 2005; Le Roux et al., 2018). In this study, the most common species detected at such open and remote locations were often hoary, big brown, evening, and eastern red bats. Hoary and eastern red bats are regarded as fast flying aerial hawkers, often found in open spaces by vegetation and sometimes at high altitude (Norberg & Raynor, 1987). Big brown, silver-haired, and evening bats will also hawk prey around cluttered and open areas (Norberg & Raynor, 1987; Jones et al., 2016). While in this study, overall activity at these remote

locations was very low, such features could serve as stepping stones and foraging opportunities as bats move through the landscape, and might also serve to draw bats further from habitat edges into open spaces (Estrada & Coates-estrada, 2001; Heim, 2017). In this study, bat use on the prairie site did not differ much from distributions on crop plots, suggesting that prior to European settlement, bat prairie use was likely restricted mostly to riparian areas and isolated trees (Holloway & Barclay, 2000; Heim et al., 2015; Treitler et al., 2016), and by fewer species (Benedict, 2004; Anderson et al., 2017).

From the limited data obtained on little brown, northern long-eared, and tri-colored bats, these species were almost exclusively detected at sites containing large amounts of tree cover, and were most active in forest interior and edge habitats. These species are regarded as clutter-adapted, capable of hawking, hover-gleaning, and trawling insects from vegetation, ground, and water surfaces (Norberg & Raynor, 1987; Ratcliffe & Dawson, 2003; Jones et al., 2016), and in North America, are among the most impacted by white-nose syndrome (Frick et al., 2015). Tri-colored bats were also the only species most active on the tallgrass prairie site than on any of the crop sites, and also frequently detected over an open corn field. Other studies have also found that even these clutter-adapted species will forage in open areas over forested, likely in instances where the overall fragmented landscape complements roosting and foraging sites (Ethier & Fahrig, 2011; Monck-Whipp et al., 2018). Silver-haired bats also appeared most often at forested sites as well as those with water present.

Big brown bats were most active within 50 meters of edge habitat and leveled off around 100 meters in open fields. Similarly, eastern red, silver-haired, and evening bats

were primarily active within 200 meters of edge habitat (Fig. 1.9). Little brown, northern long-eared, and tricolored bats were all most active at the forest edge, with minimal activity in open, arable areas. Hoary bats were also very active by habitat edges, but along with evening, big brown, and eastern red, were one of the most commonly recorded species on open habitats. Since some generalist bats are capable of flying over long distances through open landscape (Estrada & Coates-Estrada, 2002), the low number of recordings at open habitats or isolated tree cover sites could indicate these individuals are simply passing through and not necessarily foraging, or are flying at higher altitudes (Griffin & Thompson 1982; Fenton & Griffin, 1997; Frick et al., 2012) in these areas. Some bats have demonstrated the ability to change foraging behavior to take advantage of sudden insect abundances (Charbonnier et al., 2014; Maine & Boyles, 2015), even in open habitat (Müller et al., 2012) and capable of tracking migrating insect populations (McCracken et al., 2012).

Unlike bat activity, insect volume collected from light traps was not necessarily highest at the habitat edge (Table 1.5, Fig. 1.10). There seemed to be a steady decline in insect volume away from field edges at half the sites we sampled, while the other half had seemingly increases in insect availability from edge habitat, including both windbreak sites. All agricultural sites had already been treated with pesticides before sampling. Flying insects in these agricultural environments tend to be affected by wind and daily weather conditions (Lewis, 1969; Grüebler, 2008) and field distributions can vary by species (Dix et al., 1997). Similarly, such inclement weather and climate can also alter and reduce bat activity (Erickson, 2002; Parsons, 2003; Frick et al., 2012). While insects were collected during calm weather periods, my results indicate that while

insect biomass may increase, decrease, or remain the same over crop fields from tree cover, bat foraging activity primarily occurs along habitat edges with seemingly very little to no activity over crop fields. Consequently, insects and crop pests that remain in open tracts of agricultural crops or along isolated tree patches are far less likely to be consumed by bat species in the area, and continue to inflict agricultural damages. While insects were not identified in this study, insect abundance has been found to increase with higher land-use intensity, although accompanied by a decrease in insect size and diversity (Treitler et al., 2016).

Bats under laboratory conditions have demonstrated an ability to consume hundreds of insects at an hourly rate (Griffin et al., 1960; Coutts et al., 1973). Although this rate of consumption is likely not realistic in the wild, some species are capable of eating close to their own body weight each night (Charles-Dominique, 1991; Kunz et al., 1995) and bats are thought to play a major role in consuming insect pests. Studies suggest bats can save farmers billions of dollars per year in crop damage reductions (Cleveland et al., 2006; Boyles et al., 2011; Maine & Boyles 2015). However, these are national or even global extrapolations based on a few bat species in small scale studies on a single crop, or in Boyles (2011), an abundant generalist species that forms the largest concentrations of mammals on earth (McCracken, 2003) but does not inhabit most of North America. Such extrapolations assume all bats use all crop acreage equally, however many species are habitat specialized, and appear to primarily capitalize on areas with tree cover. Consequently these bats are not likely to spend considerable time consuming insects in expansive tracts of open crop monocultures. This illustrates the importance of scale, landscape connectivity, and how different species interact with their

surroundings (Tscharntke et al., 2005; Ethier & Fahrig, 2011; Treitler et al., 2016). Therefore, test results conducted in closed environments that exclude natural processes cannot always be applied to predict outcomes and behaviors in actual complex and dynamic ecosystems.

Although our study has considerable implications on the large scale monetary benefits that bats may actually provide, regardless, these creatures are still assets in consuming large numbers of insects and crop pests on a nightly basis, which undoubtedly prevents insect damage to some degree. While advantageous for bats, tree species however, if neglected or incorrectly managed, can also invade sensitive ecosystems like grasslands and prairies, which dominated states like Nebraska prior to European settlement. Eastern redcedar (*Juniperus virginiana*), a species commonly used in windbreaks, has especially caused much woody encroachment across Nebraska and surrounding states (Leis et al., 2017; Donovan et al., 2018). Such woody invasions can alter ecological structure, grassland diversity, and water availability, which in turn can lead to a loss of ecosystem services, including the disruption of grazing lands for livestock production, and an increase in wildfires (Engle et al., 1987; Twidwell et al., 2013; Donovan et al., 2018; Zou et al., 2018). Consequently, it is important to focus on species-level habitat differences and the scale of those habitat associations, in order to formulate systems-level resource management strategies.

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Tables and Figures

Table 1.1. Total bat passes by all species at each agricultural site in southeast Nebraska (n = 11). Sites are ordered from highest to lowest amounts of total call counts, which were each aggregated from a deployment session spanning 4 nights with 24 detectors. Only site 11 was not either a corn or a soybean field. Figure 1.1 contains satellite imagery for each site.

Site	Site Description	Call Count
5	windbreak and riparian forest fragment bordering soy field	12,581
1	riparian forest corridor bordering corn field	7,197
4	creek buffer that intersects corn and soy fields	5,917
11	restored tallgrass prairie bordering windbreak by riparian wooded area	3,141
7	forest fragment bordering corn and soy fields with isolated trees	2,638
2	buffer strip with pond bordering corn fields	2,563
10	corn field	1,538
9	buffer strip bordering corn fields with isolated tree patches	931
6	irrigation drainage strip bisecting soy field	803
8	isolated homestead shelterbelt in corn field intersected with grassy strips and single isolated trees	496
3	isolated windbreak bordering soy and corn fields	198

Table 1.2. Call totals for each species by sample site in rural southeast Nebraska. Counts at each site were aggregated from a deployment session spanning 4 nights with 24 detectors. Only site 11 was not either a corn or a soybean field. Dotted lines represent no detection occurrences for a particular species.

Site	Big Brown	Eastern Red	Hoary	Silver Haired	Little Brown	Northern	Evening	Tricolored
1	1534	2282	1391	135	22	111	1718	4
2	48	1560	155	12	-----	2	786	-----
3	55	31	77	7	3	-----	25	-----
4	1680	342	3257	294	2	-----	341	1
5	4987	972	4785	633	50	15	1116	23
6	132	81	381	52	-----	-----	156	1
7	397	553	678	83	47	10	851	19
8	182	34	48	19	5	-----	206	2
9	414	61	181	46	3	1	216	9
10	462	72	73	34	7	2	841	47
11	997	117	816	151	14	18	1003	25

Table 1.3. Linear regression R2 values for bat activity with respect to distance from crop field edges in southeast Nebraska. Each site was bordered by a different habitat edge type. Analysis was run using R 3.6.2, R Core Development Team. Dotted lines represent insufficient or no detection occurrences for a particular species.

Site	Big Brown	Eastern Red	Hoary	Silver Haired	Little Brown	Northern	Evening	Tricolored
1	0.19	0.18	0.43	0.34	0.36	0.44	0.13	-----
2	0.11	0.32	0.043	0.06	-----	-----	0.22	-----
3	0.43	0.49	0.045	0.023	-----	-----	0.17	-----
4	0.42	0.40	0.24	0.39	-----	-----	0.25	-----
5	0.63	0.66	0.84	0.79	1	0.84	0.67	1
6	0.028	0.076	0.19	0.028	-----	-----	0.034	-----
7	0.21	0.38	0.017	0.24	0.32	0.24	0.35	0.27
8	0.16	0.16	0.0026	0.11	0.49	-----	0.0033	-----
9	0.022	0.0056	0.091	0.003	-----	-----	0.044	0.034
10	0.15	0.0074	0.078	0.012	0.012	-----	0.098	0.085
11	0.19	0.12	0.00096	0.04	0.17	0.051	0.0022	0.27

Table 1.4. P-values and levels of statistical significance for R2 values for bat activity with increasing distance to crop field edges in southeast Nebraska. Statistical significance levels are enclosed with parentheses. Analysis was run using R 3.6.2, R Core Development Team. Dotted lines represent insufficient or no detection occurrences for a particular species.

Edge Type	Big Brown	Eastern Red	Hoary	Silver Haired	Little Brown	Northern	Evening	Tricolored
1	0.0405 (0.01)	0.0491 (0.01)	0.00096 (0)	0.018 (0.01)	0.284 (1)	0.337 (1)	0.095 (0.05)	-----
2	0.176 (1)	0.0037 (0.001)	0.334 (1)	0.4935 (1)	-----	-----	0.02 (0.01)	-----
3	0.1593 (1)	0.1865 (1)	0.6853 (1)	0.847 (1)	-----	-----	0.591 (1)	-----
4	0.00103 (0.001)	0.00163 (0.001)	0.0213 (0.01)	0.00204 (0.001)	-----	-----	0.018 (0.01)	-----
5	0.206 (1)	0.187 (1)	0.0836 (0.05)	0.111 (1)	-----	0.265 (1)	0.18 (1)	-----
6	0.437 (1)	0.2014 (1)	0.0345 (0.01)	0.457 (1)	-----	-----	0.3885 (1)	-----
7	0.0298 (0.01)	0.00176 (0.001)	0.556 (1)	0.0218 (0.01)	0.034 (0.01)	0.326 (1)	0.00296 (0.001)	0.0691 (0.05)
8	0.0669 (0.05)	0.102 (1)	0.852 (1)	0.235 (1)	0.243 (1)	-----	0.7955 (1)	-----
9	0.488 (1)	0.734 (1)	0.151 (1)	0.819 (1)	-----	-----	0.324 (1)	0.6597 (1)
10	0.0584 (0.05)	0.704 (1)	0.263 (1)	0.706 (1)	0.892 (1)	-----	0.135 (1)	0.200 (1)
11	0.0337 (0.01)	0.118 (1)	0.888 (1)	0.375 (1)	0.243 (1)	0.4569 (1)	0.827 (1)	0.0677 (0.05)

Table 1.5. Insect volumetric measurements from light traps at increasing distances from crop field edges in southeast Nebraska. Sites were sampled once over a 5 hour period beginning at sunset. Traps were placed at 20m, 220m, and 420m from crop field edges, and contents from each trap measured in a 250mL graduated cylinder. Graphs illustrated in Fig. 20.

Site	Date	(20m)	(220m)	(420m)
1	August 6	207 mL	208 mL	190 mL
5	August 8	186 mL	218 mL	242 mL
4	August 11	78 mL	40 mL	30 mL
3	August 12	212 mL	242 mL	272 mL
9	August 13	233 mL	150 mL	159 mL
11	September 3	68 mL	66 mL	98 mL
Average		164 mL	154 mL	165.17 mL

Figure 1.1. Agricultural sampling sites with borders around the rectangular extent of acoustic detector grid placements in Gage and Lancaster counties, Nebraska. All sites were corn or soybean, except site 11, which was a restored tallgrass prairie.

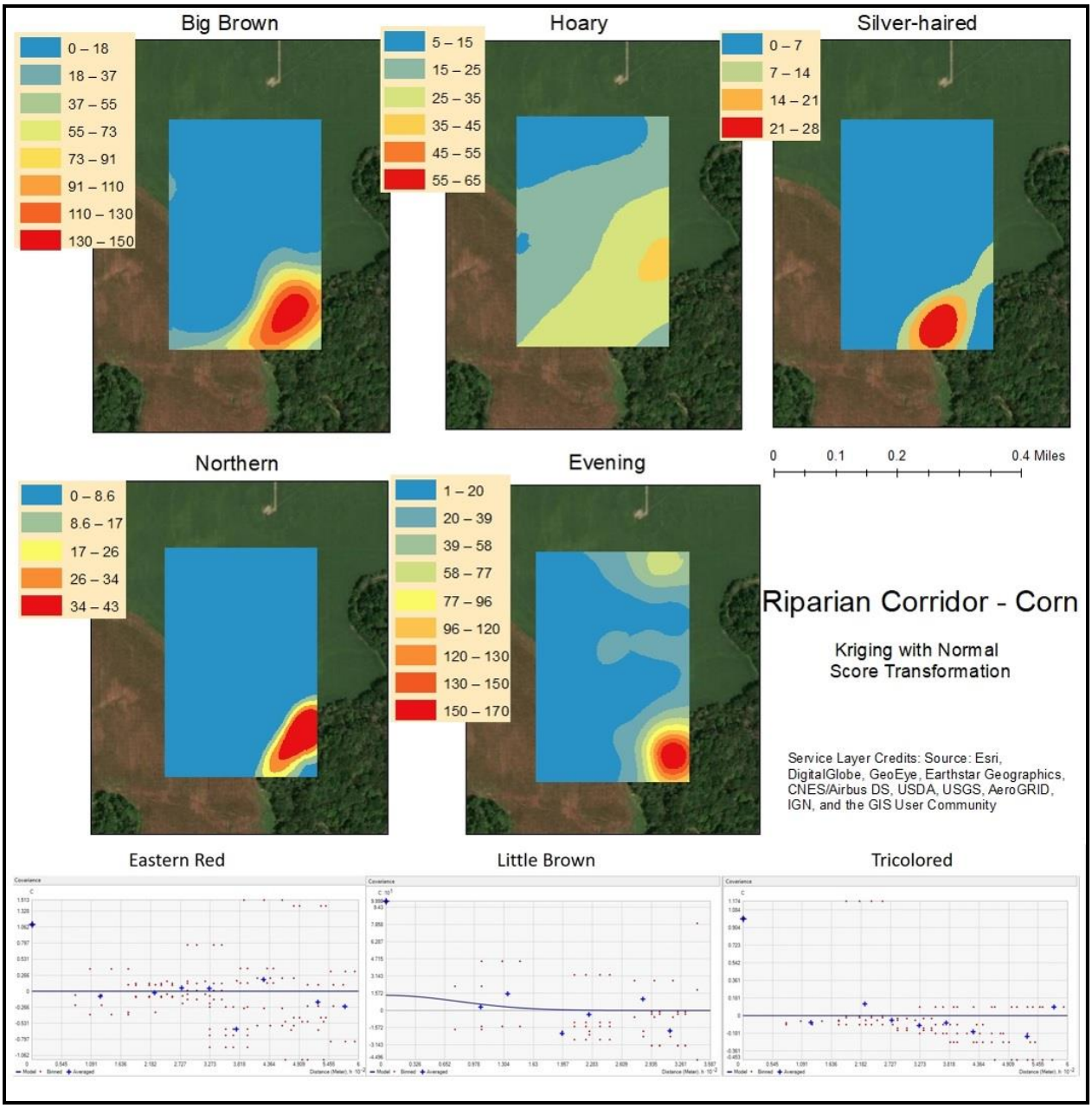

Figure 1.2. Spatial interpolation results for bat species at Site 1 in rural southeastern Nebraska. Species detected with no autocorrelation include the eastern red (2282 calls), little brown (22 calls) and tri-colored (4 calls). Most activity occurs along the forest edge, with rapid activity decline in the open corn field. Interpolation maps were made by kriging call results across 4 nights with a normal score transformation. Bins contain the call count groupings.

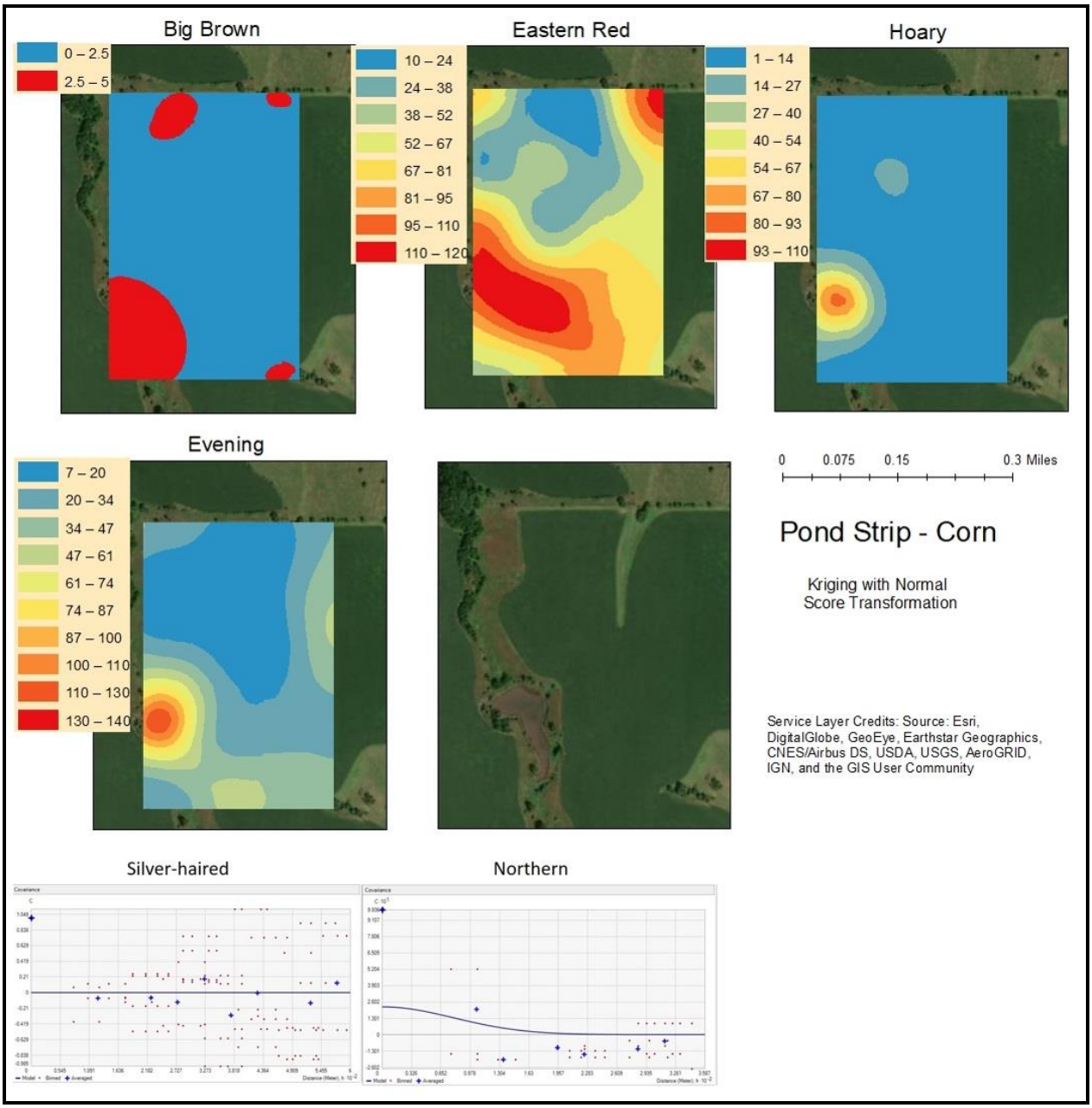

Figure 1.3. Spatial interpolation results for bat species at Site 2 in rural southeastern Nebraska. Species detected with no autocorrelation include the silver-haired (12 calls) and northern (2 calls). Most activity occurs primarily over the pond over the 4 night span. Interpolation maps were made by kriging with a normal score transformation. Bins contain the call count groupings.

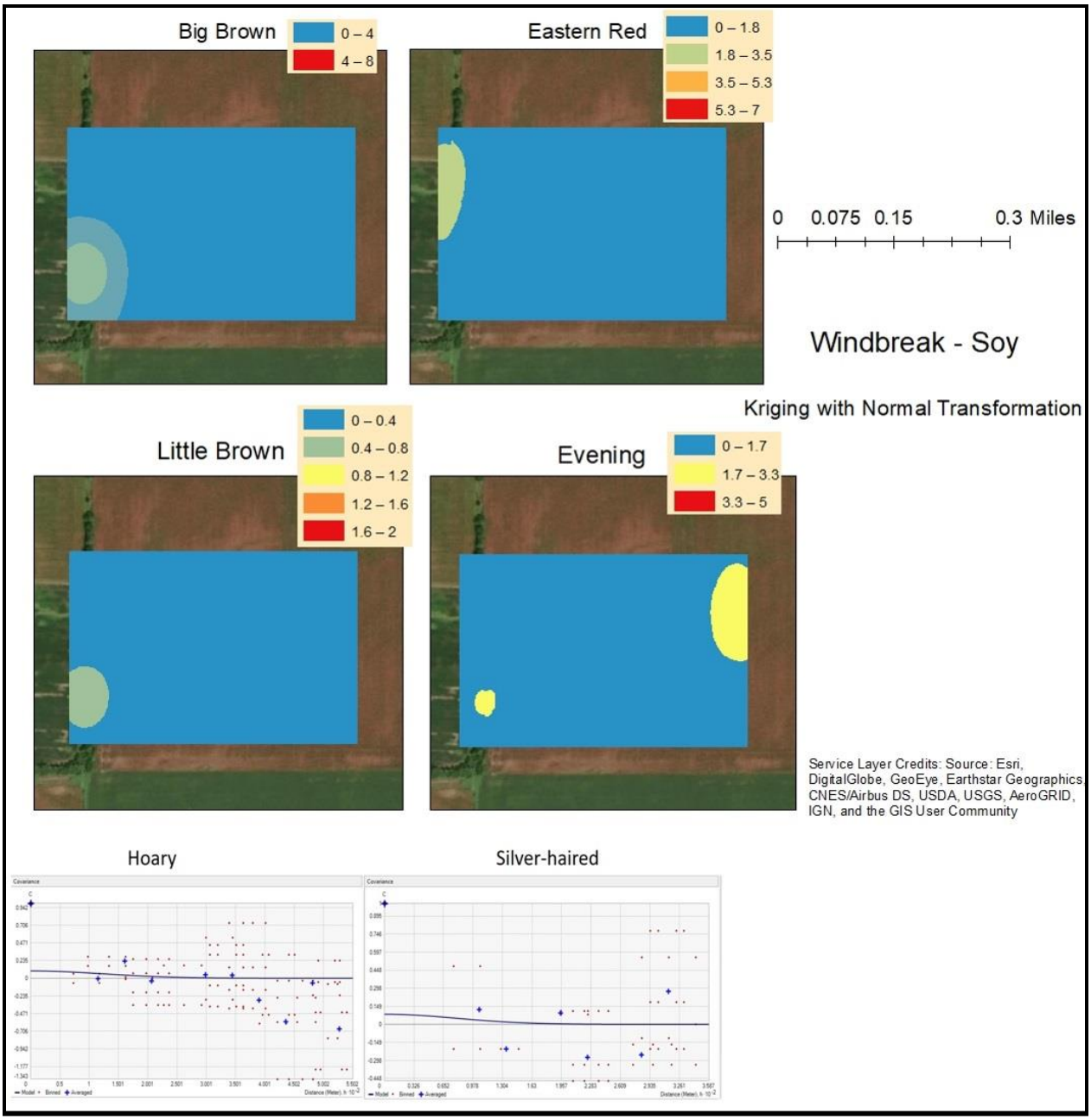

Figure 1.4. Spatial interpolation results for bat species at Site 3 in rural southeastern Nebraska. Species detected with no autocorrelation include the hoary (77 calls) and silver-haired (7 calls). Most activity occurs along the windbreak. Distributions tended to be patchy, likely due to the minimal tree cover, leading to the low numbers of calls by bats at this particular site. Interpolation maps were made by kriging call results across 4 nights with a normal score transformation. Bins contain the call count groupings.

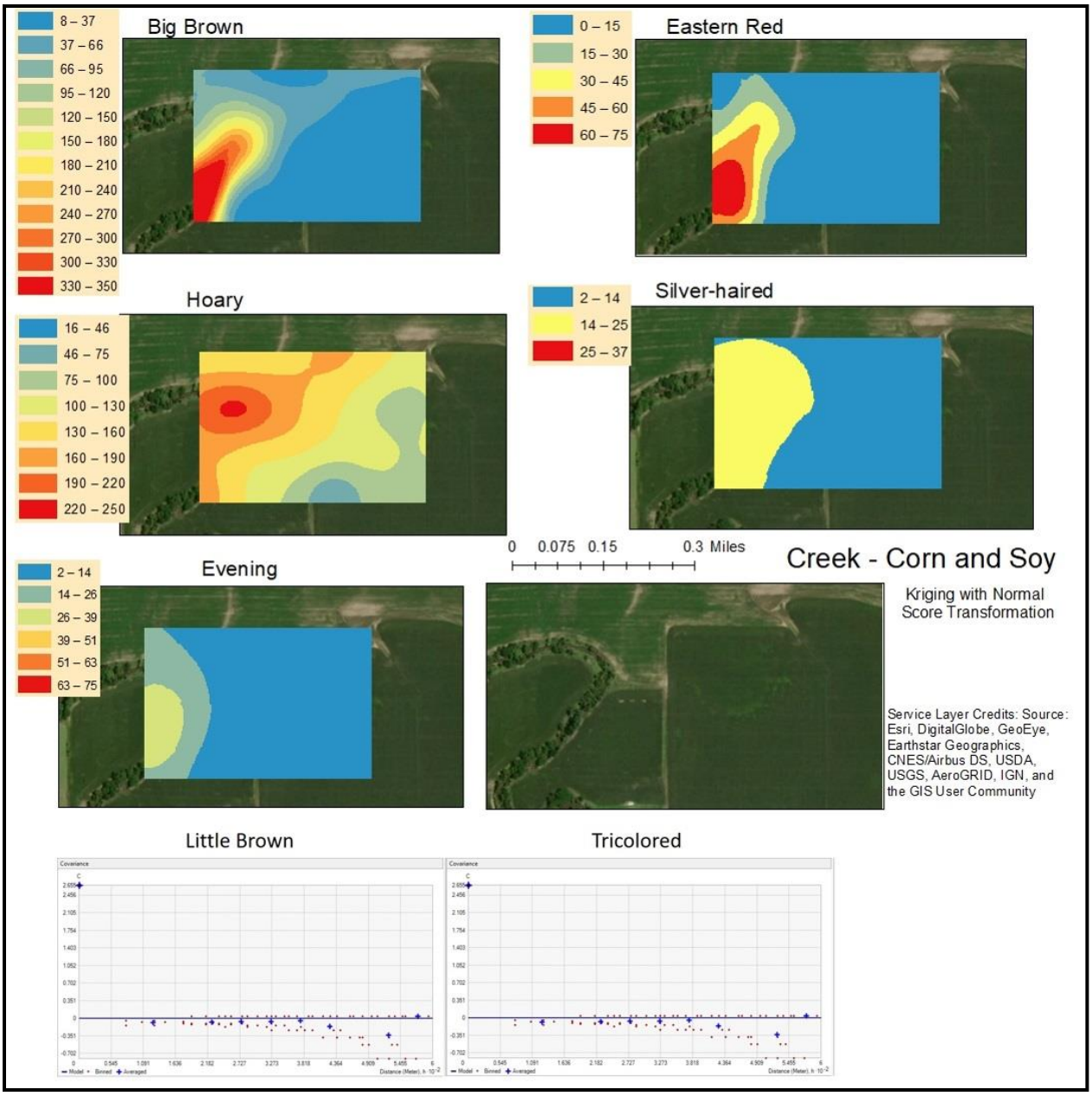

Figure 1.5. Spatial interpolation results for bat species at Site 4 in rural southeastern Nebraska. Species detected with no autocorrelation include the little brown (2 calls) and tricolored (1 call). No northern long-eared bats were recorded. Most activity occurs along the waterway, and diminishes into the open corn and soy field. Hoary and big brown appear the most likely to forage over open habitats. Interpolation maps were made by kriging call results across 4 nights with a normal score transformation. Bins contain the call count groupings. Darker green crop cover indicates soy, which transitions to corn in the upper lighter areas.

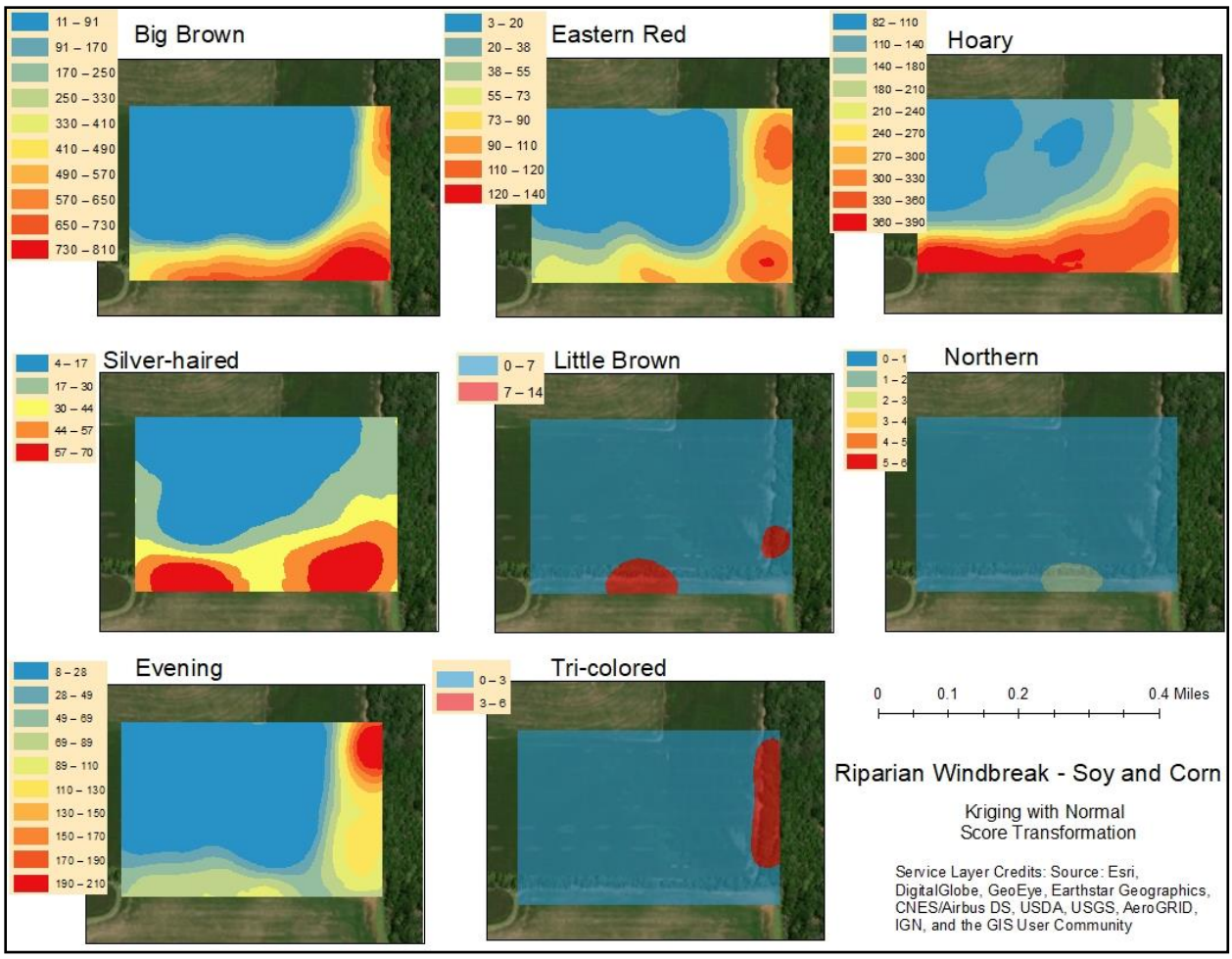

Figure 1.6. Spatial interpolation results for bat species at Site 5 in rural southeastern Nebraska. Most activity occurs along the windbreak and forest edge over the 4 night span, however, for little brown, northern, and tri-colored bats, spatial autocorrelation was very weak, as indicated by the kriging semivariogram. This is likely due in part to the low number of bat calls, which requires relatively more binning for that correlation to become visually apparent. Interpolation maps were made by kriging with a normal score transformation. Bins contain the call count groupings. Darker green crop cover indicates soy, which transitions to corn in the lighter areas.

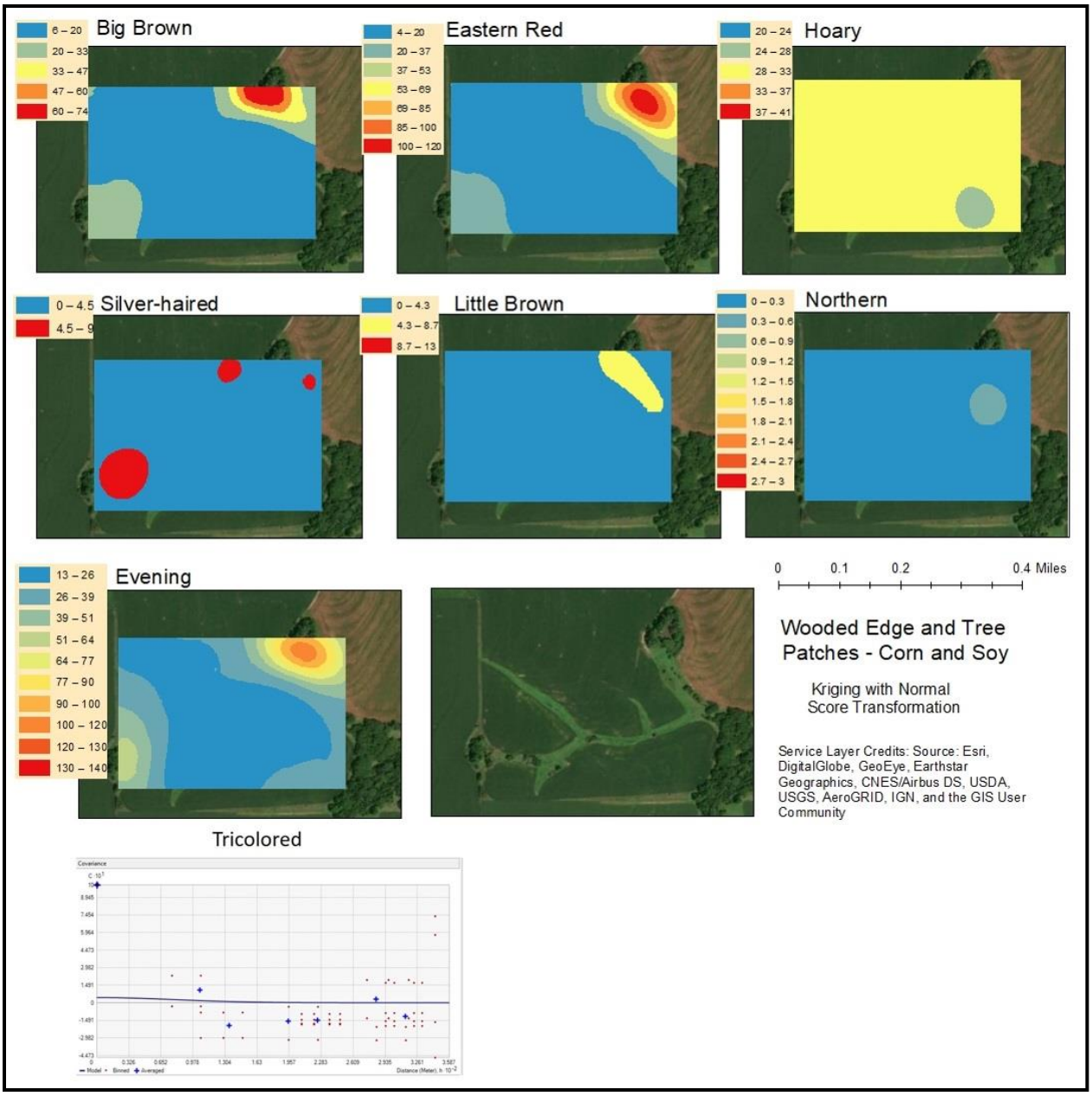

Figure 1.7. Spatial interpolation results for bat species at Site 7 in rural southeastern Nebraska. Most activity seems to be centered over a tree patch containing a small pond, but occurs also along the forest edge as well as further, more isolated tree patches by the more open adapted foraging species. Bats detected with no autocorrelation include only the tri-colored bat (19 calls). For hoary, silver-haired, little brown, and northern, spatial autocorrelation was very weak, as indicated by the kriging semivariogram. Aside from the open-adapted hoary bat, this is likely due in part to the low number of species calls, which requires relatively more binning for that correlation to become visually apparent. Interpolation maps were made by kriging with a normal score transformation. Bins contain the call count groupings. Darker green crop cover indicates corn, which transitions to soy in the lighter areas.

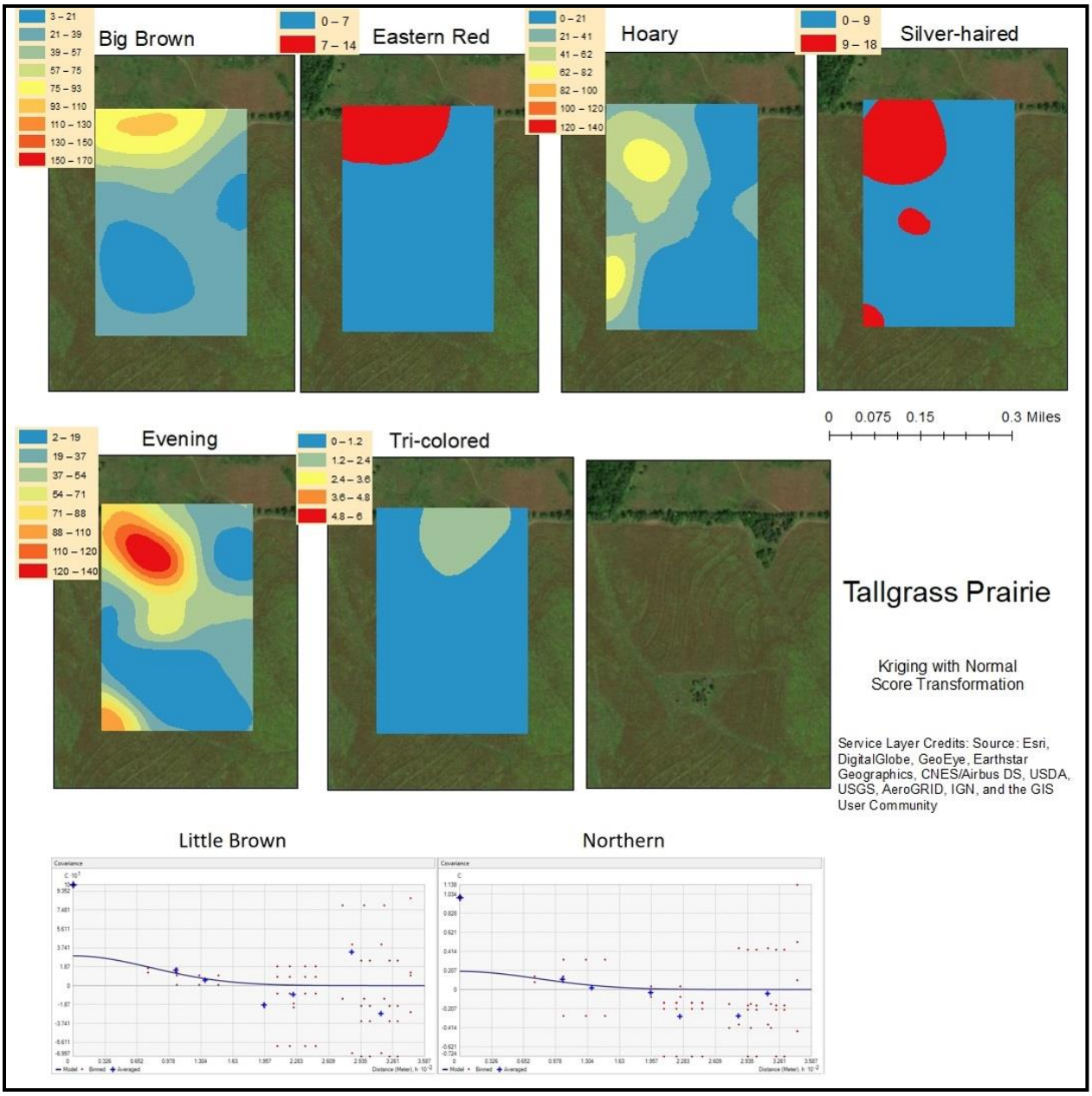

Figure 1.8. Spatial interpolation results for bat species at Site 11 in rural southeastern Nebraska. Most activity over the 4 night span occurs along the windbreak, which stems from a riparian corridor. Bats detected with no autocorrelation include little brown (12 calls) and northern (18 calls). For eastern red, silver-haired, and tricolored, spatial autocorrelation was very weak, as indicated by the kriging semivariogram. Interpolation maps were made by kriging with a normal score transformation. Bins contain the call count groupings.

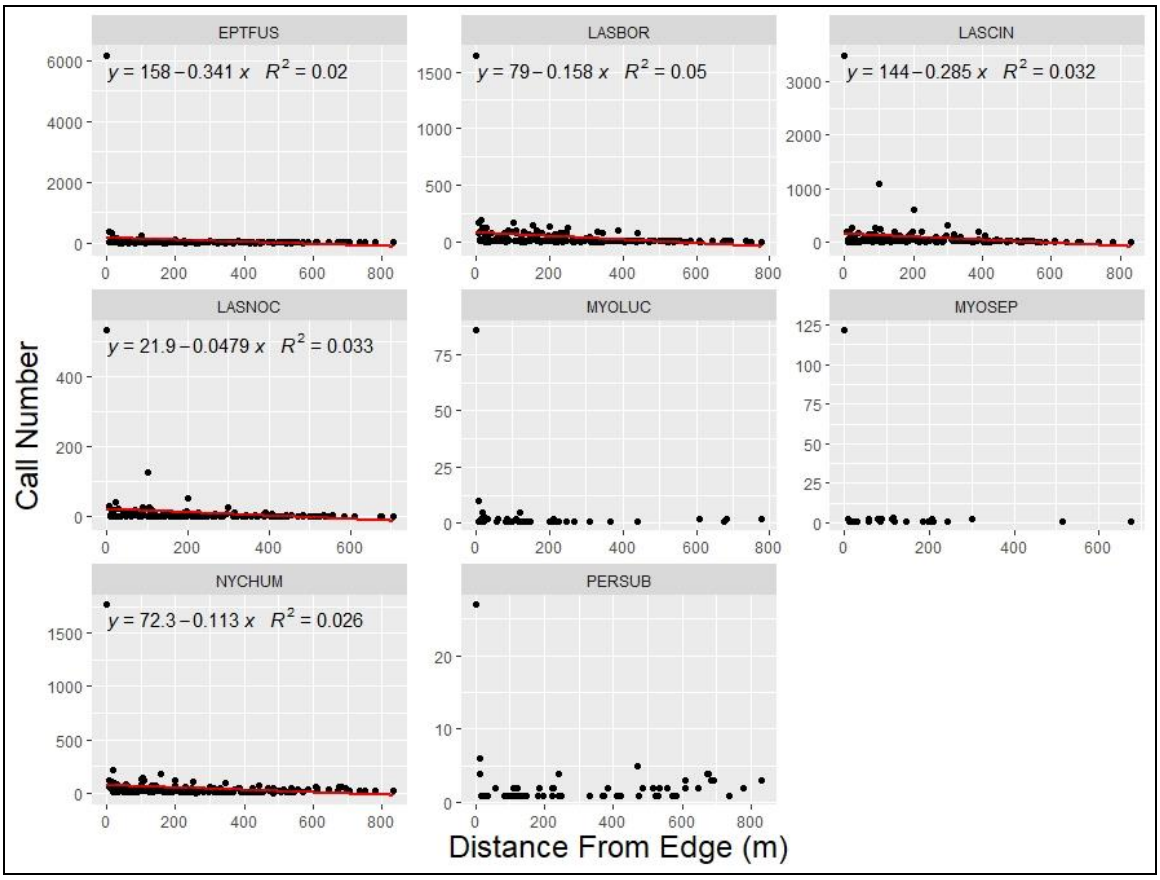

Figure 1.9. Species activity regression results from crop edge habitat across all sites in rural southeast Nebraska. R^2 was statistically significant ($p < 0.05$) for big brown (EPTFUS), eastern red (LASBOR), hoary (LASCIN), silver-haired (LASNOC), and evening (NYCHUM) bat species. See Appendix A for individual sites.

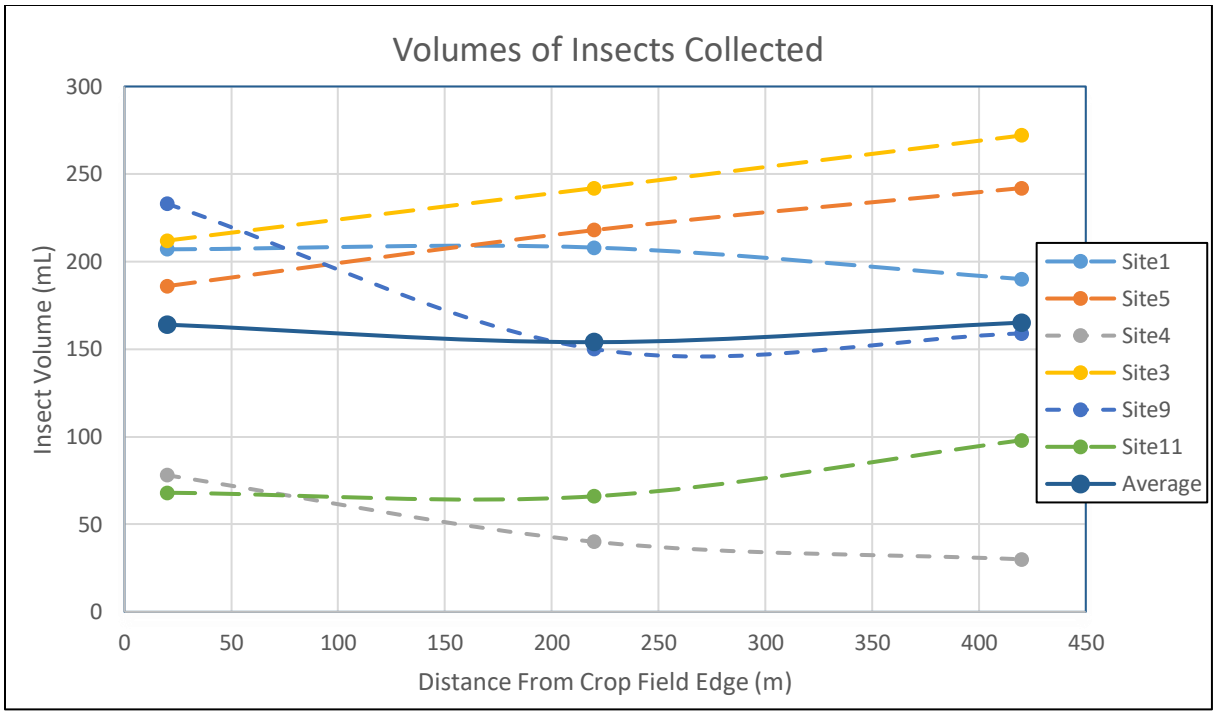

Figure 1.10. Insect volume collected at light traps placed at increasing distances from crop field edges in southeast Nebraska. Sites were sampled once over a 5 hour period beginning at sunset. Traps were placed at 20m, 220m, and 420m from crop field edges. Contents from each trap were measured in a 250mL graduated cylinder. Exact measurement values are contained in Table 5. The solid line denotes the average volume of all sites.

CHAPTER 2: SPATIAL AND TEMPORAL RELATIONSHIPS BETWEEN BAT SPECIES FORAGING IN AGRICULTURAL LANDSCAPES

Abstract

Interactions among organisms are an important component of species behavior in human-altered landscapes. To investigate spatial and temporal relationships between species in an intensively managed agricultural landscape, I used a novel acoustic grid setup that I deployed along various crop field edges in southeast Nebraska. I sampled each plot once over a period of four nights, and documented eight bat species, none of which had any significant negative spatial or temporal relationships. Additionally, I also found high degrees of temporal overlap for all species pairwise comparisons through the novel application of camera trap analytical methods on acoustic data. However, despite these findings, niche partitioning may still be taking place, likely in vertical space or based on prey species consumed. Since these environments are likely to increase across the globe, more research is needed to better understand how bat species interact with one another and the landscape to allow for their persistence in these extreme ecosystems.

Introduction

Interactions among organisms are an important component of species behavior and a driver of community dynamics, especially in human-altered landscapes (Gil et al., 2018). The conversion of natural habitats by humans for agricultural production can change patterns of resource availability (Matson et al., 1997), and likely cause increased competition between wildlife species. The introduction of fertilizers and pesticides that often accompanies such rapid crop yield expansion can also jeopardize natural ecosystem services. In agricultural landscapes, bats provide ecosystem services by consuming

insects (Kunz et al., 2011), and hunt through a variety of foraging behaviors and morphological adaptations that could reduce species competition and facilitate coexistence (Norberg & Rayner, 1987; Schnitzler & Kalko, 2001; Denzinger & Schnitzler, 2013).

Given the cryptic nature of bats, species are often grouped in classes or guilds based on similarities in morphology, echolocation, and foraging strategy to predict behavior (Aldridge & Rautenback, 1987; Norberg & Raynor, 1987; Denzinger et al., 2016). Foraging bats that rely on echolocation to navigate and catch insects and other airborne prey on the wing are termed "aerial hawkers" (Schnitzler et al., 2003; Jones et al., 2016). These species have morphological traits and echolocation call structures that enable them to hunt in open and a variety of edge and background-cluttered spaces (Norberg & Raynor, 1987; Schnitzler & Kalko, 2001). Other species are more suited for patrolling high-clutter areas, and are capable of "gleaning" insects off a variety of surfaces in addition to hunting on the wing, performing such techniques as trawling for prey over water or feeding from a perch, termed "flycatching" (Norberg & Rayner, 1987; Schnitzler & Kalko, 2001; Ratcliffe & Dawson, 2003; Jones et al., 2016). Wing morphology and echolocation abilities have also been shown to predict not only habitat tendencies, but also species vertical niche in airspace (Roemer et al., 2019).

Other bat species are more subtle with or minimalize echolocation to sneak up on prey (Fiedler, 1979), and although still important for finding food (Denzinger et al., 2016), frugivorous and nectarivorous bats rely less on echolocation for orientation purposes (Jones & Teeling, 2006). Studies have shown many species will tune in, or "eavesdrop" on the echolocation calls of other bats to gain information (Barclay, 1982;

Ubernickel et al, 2013, Jones et al., 2016; Lewanzik et al., 2019). Eavesdropping can assist individuals find active feeding areas and communal roosting sites with other bats, and provide information about species, age, identity, and reproductive condition, helping fine-tune decision making and determining if further interaction is beneficial (Fenton & Morris, 1976; Barclay, 1982; Masters 1995; Gillam & Fenton, 2016; Lewanzik et al., 2019). Such calls can be used to "claim" food from other bats and better capture prey (Wright et al., 2014).

When feeding, some bats appear to have foraging grounds and feeding routes that they frequent (Kunz, 1973; Lemke, 1984), and will even exhibit territorial behavior (Bradbury & Vehrencamp, 1977; Lemke, 1984). Several species also have high roost fidelity (Lewis, 1995). Sympatric species have been found to partition space and time (Kunz, 1973; Aldridge & Rautenback, 1987; Mancina et al., 2012), especially for limited resources (Adams & Thibault, 2006; Razgour et al., 2011; Lambert et al., 2018), which likely facilitates coexistence. Changes in behavior to accommodate resource use by multiple species through temporal resource partitioning could allow for decreased competitive interactions, but is seldom tested (Salinas-Ramos et al., 2020). Many mammalian studies rely on camera traps for data collection, and employ a temporal overlap method to determine niche partitioning among mammalian predators (Ridout & Linkie, 2009, Ridout & Linkie, 2011). However, this method has not been performed on bat acoustic data to analyze species temporal relationships.

The purpose of this study is to examine the spatial and temporal relationships between foraging insectivorous bat species in the agricultural landscape of southeastern Nebraska. Intensification of cropland is an accelerating phenomenon that creates

monoculture areas that virtually eliminate native habitats (Daily & Ehrlich, 2001; Tscharntke et al., 2005; Meehan et al., 2011), limiting options for some wildlife, but allowing for the range expansion of others (Benedict, 2004; Anderson et al., 2017). I hypothesized that spatial and temporal partitioning would occur among bat species across our sampling sites. I predicted that areas with larger amounts of tree cover would have larger amounts of spatial co-occurrence between species, since forest fragments are a limited resource in intensively farmed landscapes. I predicted temporal partitioning to occur between species, with higher temporal overlap among species that forage primarily in clutter.

Methods

Study Area

I conducted this research across 10 cropland sites and 1 restored prairie in Gage and Lancaster counties in rural southeast Nebraska. The agricultural sites were privately owned and managed by different landowners, while the prairie restoration was maintained by the National Park Service. The area is heavily managed for the production of corn and soybean primarily, and characterized by large tracts of open farmland on flat, upland plains, interspersed with riparian buffers, windbreaks, and patches of mature lowland forest. Prior to European settlement, this area was predominately a tallgrass prairie ecosystem. I selected crop fields that were at least partially bordered by some form of tree cover or other natural habitat feature, since these natural areas are often used by bats in agricultural landscapes. I also included two sites with no immediate habitat edge to gather additional information on activity over expansive crop fields.

Data Collection

I used AnaBat Express passive zero cross acoustic detectors (Titley Scientific, Brendale, QLD, Australia, www.titleyscientific.com) to record bat activity. Each Express unit has a maximum optimal range of 50 meters, so I used ArcGIS to create a layer of points each 100 meters apart to form a transect grid that bordered the habitat feature and extended into the crop field (Fig. 2.1), spanning a detection area 400 meters by 600 meters that employed 24 detectors (Mtsetfwa et al., 2018). I then entered the coordinates for these locations into hand-held Garmin GPSMAP 64 units for actual detector placement in the field.

I mounted each detector on a modified painter's pole extended 4 meters above the ground so all units cleared any ground cover for increased recording quality (Mtsetfwa et al., 2018). I positioned detectors such that every unit's omnidirectional microphone faced into the open and away from tree clutter. I left detectors at each deployment site for 4 consecutive nights, with each detector set to begin recording from at least 30 minutes before sunset until 30 minutes after sunrise. If there was sustained heavy rain, low temperatures, or high winds during a deployment session, I left detectors for additional nights as needed, until 4 sampling nights with optimal weather conditions were obtained. Issues with battery life occurred on two sites, so I redeployed problem units and a combination of different nights were used in both cases, using as many identical nights as possible across detectors. Sampling took place from June through August.

Acoustic Analysis

I downloaded acoustic detector files and analyzed with AnalookW software (Titley Scientific) (Mancina et al., 2012; Fuentes-Montemayor et al, 2013) to convert

files to individual "bat passes" for further analysis. I analyzed all recordings using Kaleidoscope v5.1.9 with the Bats of North America 5.1.0 classifier set to "+1 More Accurate" (Wildlife Acoustics, Concord, MA, USA; www.wildlifeacoustics.com). I used Kaleidoscope's recommended default signal parameters as follows: 8-120kHz frequency range, 2-500ms length of detected pulses, 500ms inter-syllable gap, 2ms minimum number of pulses, and activated the advanced signal processing feature. Under the Bats of North America 5.1.0 classifier, the selected species included in the identification process were: big brown bat (*Eptesicus fuscus*), eastern red bat (*Lasiurus borealis*), hoary bat (*Lasiurus cinereus*), silver-haired bat (*Lasionycteris noctivagans*), little brown myotis (*Myotis lucifugus*), northern myotis (*Myotis septentrionalis*), evening bat (*Nycticeius humeralis*), and tricolored bat (*Perimyotis subflavus*). Silver-haired bats were included since this species is no longer regarded as strictly migratory across the state (Benedict, 2004). However, Brazilian free-tailed bats (*Tadarida brasiliensis*) are rarely found in Nebraska, so this species was excluded from the identification analysis (Genoways et al., 2000). Kaleidoscope Pro looks for unique characteristics in the acoustic calls that makes the identification process of calls to species more feasible, and also outputs the presence probability of a particular species (Willcox et al., 2017). By summing up the numbers of identified acoustic "bat pass" files, I obtained an index of bat species activity by location and time.

Statistical Analyses

I conducted all analyses in R (3.6.2, R Core Development Team), and created spatial and temporal correlation matrices to investigate statistically significant relationships between bat species. For spatial analysis I tested all sites together, as well

as each site separately (Appendix B), since the amount of field edge habitat varied between each site. I included data from all sites for temporal analyses, dividing time into hourly and 15 minute increments. Since most bat species data were not normally distributed and contained outliers, I used the non-parametric Spearman Rank Correlation method over the Pearson Correlation test to conduct these analyses.

Additionally, I used the R package "overlap" (Ridout & Linkie 2009) to investigate temporal activity patterns of bats and the degree of overlap between species. This package compares kernel density estimates of species activity over time, uses the Rao's Spacing Test for bat data uniformity, and calculates a coefficient of overlapping ranging from 0 to 1, while generating confidence intervals through bootstrapping (Ridout & Linkie, 2011). I used the recommended smoothing factor of 1 for larger observation counts, and set 10,000 bootstrap samples for each species comparison (Ridout & Linkie, 2009).

Results

Spatial Correlation

Across sites, bat species spatial use of agricultural fields in pairwise comparisons (ρ) was positively correlated (Fig. 2.2), and only positive correlations were statistically significant ($p < 0.05$). Overall, sites with more woody cover and water availability had stronger positive co-use between bat species than those with little edge habitat, such as sites 2, 3, 6, 8, and 9, where most spatial correlations were statistically insignificant (Appendix B). While site 8 also had the only instance of significant spatial negative correlation between any species, tricolored and eastern red ($\rho = -0.42$), only 2 tricolored calls were recorded to the 34 eastern red over the 4 night stretch. Among the more open

foraging bat species, positive relationships still occurred between big brown and eastern red at site 8 ($\rho = 0.53$), hoary and silver-haired at site 6 ($\rho = 0.56$), eastern red and evening at site 2 ($\rho = 0.73$), and both eastern red and evening ($\rho = 0.54$) and hoary and silver-haired ($\rho = 0.54$) at site 10 (Appendix B). These species were also the most regularly present at such sites with little edge habitat, suggesting that they will regularly venture over open habitats (Table 2.2).

Temporal Correlation and Overlap

Temporal correlations between bat species were also positively correlated. All bat species had positive temporal relationships on an hourly basis (Appendix B). When analyzing activity levels in 15 minute increments (Fig. 2.3), temporal relationships were still positively correlated, although despite eastern red and evening having a strong temporal association ($\rho = 0.74$), values remained lowest between those species with all other bats ($\rho < 0.6$). Temporal overlap results also indicated positive temporal relationships between species, with all pairwise overlap coefficients above $\Delta = 0.59$ (Table 2.3). Rao's Spacing Test confirmed that the temporal activity patterns of all bats were not uniform, as all occurring species were nocturnal.

Collectively, total bat activity was bimodal in nature, with the first and highest peak around 22:00, shortly after sunset, and a second lesser peak before sunrise at 4:00. Individual species across sites did take on bimodal shapes as well overall, as did the species kernel density estimation plots. Hoary bats were the only species detected before sunset, between 19:00 and 20:00. Big brown, eastern red, and evening bats were first detected an hour later, between 20:00 and 21:00. Little brown, northern long-eared, silver-haired, and tricolored were not recorded until after 21:00, however, these four

species were also the least detected. 15 minute and minute grouped graphs also reflect this pattern, and illustrate the more sporadic nature and limited recordings of the little brown, northern long-eared, and tricolored bats, all species associated with forest habitats.

Discussion

To my knowledge, this is the first study to utilize camera trap analytical methods on bat acoustic data, as well as sampling through extensive acoustic grids. Acoustic pairwise comparison results indicated that all bat species seemingly co-occur in time and space without any significant negative relationships. While it is possible these bats are partitioning resources in other ways, these findings bode well for bats persisting in an intensively managed agricultural landscape despite the co-use of limited shared resources.

Southeastern Nebraska lies on the edge of a number of bat species geographical ranges, including the tricolored, little brown, and northern long-eared species (Benedict, 2004). Between the eleven sites activity was recorded from all eight other species known to occur in the area. Sites with the most edge habitat had the most bat activity (Table 2.1), and lesser detected species including little brown, northern long-eared, and tricolored were mostly detected at forested sites (Table 2.2), although site 10, an open corn field with no habitat edge, appeared to have a significant amount of tricolored bat activity (Table 2.2). Little brown, northern long-eared, and tricolored bats are generally regarded as narrow and edge space foragers due to short wings and high maneuverability, capable of tracking down insects on the wing as well as gleaning prey off surfaces (Norberg & Rayner, 1987; Schnitzler & Kalko, 2001; Ratcliffe & Dawson, 2003;

Denzinger et al., 2016). However, even these clutter-adapted species have been found in open areas rather than forested, likely in instances where the overall fragmented landscape complements roosting and foraging sites (Ethier & Fahrig, 2011; Monck-Whipp et al., 2018). Little browns have also been documented trawling for insects over water surfaces (Norberg & Rayner, 1987; Clare et al., 2011). While all species were most active around forest edges (see chapter 1), hoary, big brown, evening, and eastern red bats were the main species detected at both sites with little edge habitat and around isolated woody structures. These species are primarily aerial hawkers and are seemingly able to forage in a variety of habitats, with hoary and eastern red also capable of fast flight even at altitude (Norberg & Rayner, 1987; Jacobs, 1999; Agosta, 2002; Menzel et al., 2005).

In addition to high edge habitat use among bats, results indicated that all statistically significant species pairwise comparisons were positive (Fig 2.2), with ρ values varying among the different sites (Appendix B). The most and highest positive coefficients ($\rho > 0.8$) occurred at sites 1, 4, 5, and 11 (Appendix B). These four sites all had water sources accessible to bats, as well as adjacent or nearby forest fragments (Fig. 2.1). Across these four sites, correlations were often highest ($\rho > 0.8$) between big brown, hoary, and silver-haired bats, as well as between big brown, evening, and eastern red. Curiously, these relationships were not as strong among those species at site 7 (Appendix B), which also had an adjacent forest fragment and available water sources (Fig. 2.1). Contrary to my hypothesis, overall spatial correlations appeared lower among species with little brown, northern long-eared, and tri-colored bats, although little browns did have higher correlations ($\rho > 0.7$) at site 5 (Appendix B), where they were most active

(Table 2.2). The low recording numbers I obtained on these species however makes it difficult to make any comparative conclusions between them. Low call counts could be causing these low relationship values, and the fact our detector deployments prioritized open and edge areas minimized the number of units in closed habitats, likely lessening the likelihood of picking up these high-clutter bats. Interestingly enough, only site 1 had detectors in forested habitat, and documented the most northern long-eared bat activity of all sites (Table 2.2).

Bat activity at sites with little edge habitat tended to be dispersed and uniform. These sites had relatively little activity overall, and the bats documented were primarily that of edge and open foraging species, which can likely take advantage of sudden increases of insects (Charbonnier et al., 2014; Maine & Boyles, 2015), or are merely traveling to other habitat fragments to forage. Although negative spatial relationships did exist between species, none were statistically significant at any sites, indicating no notable spatial partitioning taking place. Other studies have reported similar findings (Bell, 1980; Mancina et al., 2012), while others have found bats to exhibit spatial partitioning behavior through differential habitat use, and even in areas with limited resources (Aldridge & Rautenbach, 1987; Saunders & Barclay, 1992; Arlettaz, 1999; Nicholls et al., 2006; Razgour et al., 2011).

Similarly, temporal correlations between species were all positive when activity was viewed in 60 (Appendix B) and as well as 15 minute increments (Fig. 2.3), suggesting no temporal partitioning between species. The coefficients of overlapping (Δ) also resulted in only positive values, indicating high degrees of temporal overlap between all species (Table 2.3). Evening bats had the lowest temporal overlap ($\Delta < 0.72$) with all

species except eastern red bats ($\Delta = 0.83$). Only eastern red bat overlap with northern long-eared ($\Delta = 0.69$) and tri-colored ($\Delta = 0.71$) bats were lower. In line with my hypothesis, amounts of temporal overlap were also high among the lesser detected forest-associated little brown, northern long-eared, and tri-colored species ($\Delta > 0.85$). However, these results also suggest no temporal partitioning is taking place. Other studies have reported similar findings (Bell, 1980; Fenton &Thomas, 1980; Saunders & Barclay 1992; Presley et al., 2009), as well as other instances of temporal partitioning among bat species (Kunz 1973; Adams & Thibault, 2006; Mancina et al., 2012, Jachowski et al., 2014; Lambert et al., 2018). However, it is also possible that since these bats were only active for approximately half the diurnal cycle, that these temporal overlap values merit evaluation in a different light than overlap guidelines that focus on mammals with more uniform activity cycles.

In Fig. 2.14 – 2.16, both eastern red and evening bats peak first at 21:00, an hour before all other species, and again at 5:00, while all other species activity levels were low and on the decline, suggesting possible temporal partitioning. Hoary bats were the only species recorded before 20:00 (Fig. 2.14), and as high flying, open foragers, could be emerging before sunset to cover more ground, which likely also exposes them to more daytime predators. The majority of species in this study have been found to consume primarily Lepidoptera and Coleoptera (Brack & Whitaker, 2001; Clare et al. 2009; Valdez & Cryan, 2009; Clare et al., 2014), although little browns seemingly prefer Diptera from rivers and streams (Anthony & Kunz, 1977; Clare et al., 2011). However, these species are all generalists, and will adjust their diet to insects available as seasons change (Jacobs, 1999; Carter et al, 2003; Carter et al., 2004; Clare et al., 2009; Valdez &

Cryan, 2009; Valez & Cryan, 2013; Clare et al., 2014), as well as by geographic region (Agosta, 2004; Kaupas & Barclay, 2018). Smaller bats generally eat smaller insects (Ross, 1967; Aldridge & Rautenbach, 1987), and bats that feed in similar habitats hunt similar insect prey (Aldridge & Rautenback, 1987). Flying insects, especially in these agricultural environments, tend to be affected by wind and daily weather conditions (Lewis, 1969; Grüebler, 2008) and field distributions can vary by species (Dix et al., 1997). However, such inclement weather and climate can also alter and reduce bat activity (Erickson & West, 2002; Parsons et al., 2003; Frick et al., 2012). Such quick changes in resource availability can certainly be a recipe for species competition, and could be the case behind other studies that have found temporal partitioning to occur even within individual nights (Kunz, 1973; Hayes, 1997; Adams & Tibault, 2006). Roosting sites, especially in agriculturally dominated landscapes, can also be a source of species competition, although supporting literature evidence is limited (Salinas-Ramos et al., 2020).

Although I found little evidence for spatial and temporal partitioning between species in this study, bats are unique in that, as the only flying mammals in the world, they can perceive and utilize their environment in multiple dimensions. Consequently, it is possible that partitioning in space or time could have occurred without my detection. I recorded the highest levels of activity by all species along habitat edges, which are a limited resource in agricultural landscapes. This resulted in high spatial overlap among most species for these limited and likely contested areas. Bats are known to utilize upper airspace however, at high altitudes and over forest canopy, and out of range of my ground-based detectors (Griffin & Thompson, 1982; Fenton & Griffin, 1997; Menzel et

al., 2005), and likely partition in vertical space (Roemer et al., 2019). Since these bat species also rely largely on echolocation to navigate, species with similar call bandwidths may also partition acoustic space (Salinas-Ramos et al., 2020) and shift call frequency to avoid acoustic jamming (Gillam et al, 2007). Vegetation structure also influences bat space use (Crome & Richards, 1988; Arlettaz, 1999). Species could additionally partition based on body size or according to spatial and temporal changes in insect prey distributions (Ciechanowski et al., 2008) along crop fields.

These results indicate positive spatial and temporal relationships between all bat species that occurred in this study area, with no significant negative associations between species. To my knowledge, this was also the first use of camera trap analysis techniques on bat acoustic data, which revealed temporal overlap to occur between all bat species, indicating no apparent temporal niche partitioning taking place. All species, even open foragers, appear to capitalize on edge habitats, a limited commodity in intensively farmed landscapes, and seemingly coexist without any significant avoidance for each other.

These findings provide some insight into the relationships between how multiple species co-utilize agricultural fields. Such intensively modified landscapes can increase competition for limited resources. Since these environments are increasing globally, more research is needed to better understand how bat species interact with one another, the landscape, and their insect prey, allowing us to better conserve and allow these creatures to persist in these extreme ecosystems.

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Tables and Figures

Table 2.1. Total bat passes by all bat species at each agricultural site in southeastern Nebraska (n = 11). Sites are ordered from highest to lowest amounts of total call counts, which were each aggregated from a deployment session spanning 4 nights with 24 detectors. Only site 11 was not either a corn or a soybean field.

Site	Site Description	Call Count
5	windbreak and riparian forest fragment bordering soy field	12,581
1	riparian forest corridor bordering corn field	7,197
4	creek buffer that intersects corn and soy fields	5,917
11	restored tallgrass prairie bordering windbreak by riparian wooded area	3,141
7	forest fragment bordering corn and soy fields with isolated trees	2,638
2	buffer strip with pond bordering corn fields	2,563
10	corn field	1,538
9	buffer strip bordering corn fields with isolated tree patches	931
6	irrigation drainage strip bisecting soy field	803
8	isolated homestead shelterbelt in corn field intersected with grassy strips and single isolated trees	496
3	isolated windbreak bordering soy and corn fields	198

Table 2.2. Call totals for each bat species by sample site in rural southeastern Nebraska. Counts at each site were aggregated from a deployment session spanning 4 nights with 24 detectors. Only site 11 was not either a corn or a soybean field. Dotted lines represent no detection occurrences.

Site	Big Brown	Eastern Red	Hoary	Silver Haired	Little Brown	Northern	Evening	Tricolored
1	1534	2282	1391	135	22	111	1718	4
2	48	1560	155	12	-----	2	786	-----
3	55	31	77	7	3	-----	25	-----
4	1680	342	3257	294	2	-----	341	1
5	4987	972	4785	633	50	15	1116	23
6	132	81	381	52	-----	-----	156	1
7	397	553	678	83	47	10	851	19
8	182	34	48	19	5	-----	206	2
9	414	61	181	46	3	1	216	9
10	462	72	73	34	7	2	841	47
11	997	117	816	151	14	18	1003	25

Table 3.3. Temporal pairwise correlation coefficient comparisons of bat species at agricultural sites in southeastern Nebraska to evaluate temporal partitioning. Measurements include the coefficient of overlapping (Δ) and temporal matrix coefficients (ρ) for both hourly and 15 minute time increments. Values with x are statistically insignificant. Data suggests no temporal partitioning taking place.

Species	**Δ**	**95% bootstrap CI (basic0)**	**Hourly Matrix (ρ)**	**15min Matrix (ρ)**
LACI – LANO	0.950670092	0.93 – 0.97	0.96	0.91
PESU – MYSE	0.903450147	0.82 – 0.96	0.88	0.60
MYLU – PESU	0.896213446	0.81 – 0.95	0.92	0.60
EPFU – LACI	0.890670328	0.89 – 0.90	0.97	0.92
EPFU – LANO	0.889190231	0.87 – 0.91	0.96	0.92
LACI – MYLU	0.889059885	0.84 – 0.93	0.90	0.73
MYLU – MYSE	0.862998021	0.78 – 0.93	0.85	0.65
LANO – MYLU	0.8598209	0.80 – 0.92	0.86	0.78
LACI – PESU	0.834893129	0.77 – 0.89	0.91	0.72
LABO – NYHU	0.829493782	0.81 – 0.85	0.92	0.74
EPFU – MYLU	0.827313764	0.79 – 0.87	0.89	0.82
LANO – PESU	0.81095597	0.74 – 0.88	0.94	0.73
LABO – MYLU	0.8101183	0.76 – 0.86	0.65	0.60
LACI – MYSE	0.794571611	0.73 – 0.85	0.82	0.76
LANO – MYSE	0.785534662	0.71 – 0.85	0.85	0.73
EPFU – PESU	0.774597832	0.72 – 0.83	0.92	0.74
LABO – LACI	0.760083361	0.75 – 0.77	0.57	0.47
LABO – LANO	0.752649811	0.73 – 0.77	0.54 - x	0.52
EPFU – LABO	0.73745728	0.72 – 0.75	0.54 - x	0.50
EPFU – MYSE	0.735169893	0.68 – 0.79	0.79	0.70
LABO – PESU	0.718202844	0.66 – 0.78	0.55 - x	0.39
MYLU – NYHU	0.715593359	0.66 – 0.76	0.65	0.49
EPFU – NYHU	0.701698747	0.69 – 0.71	0.66	0.50
LACI – NYHU	0.687249512	0.67 – 0.70	0.68	0.47
LABO – MYSE	0.686990584	0.63 – 0.74	0.47 - x	0.38
LANO – NYHU	0.685432417	0.66 – 0.71	0.66	0.50
NYHU – PESU	0.61134487	0.55 – 0.67	0.58	0.24 - x
NYHU - MYSE	0.592483134	0.54 – 0.65	0.51	0.29

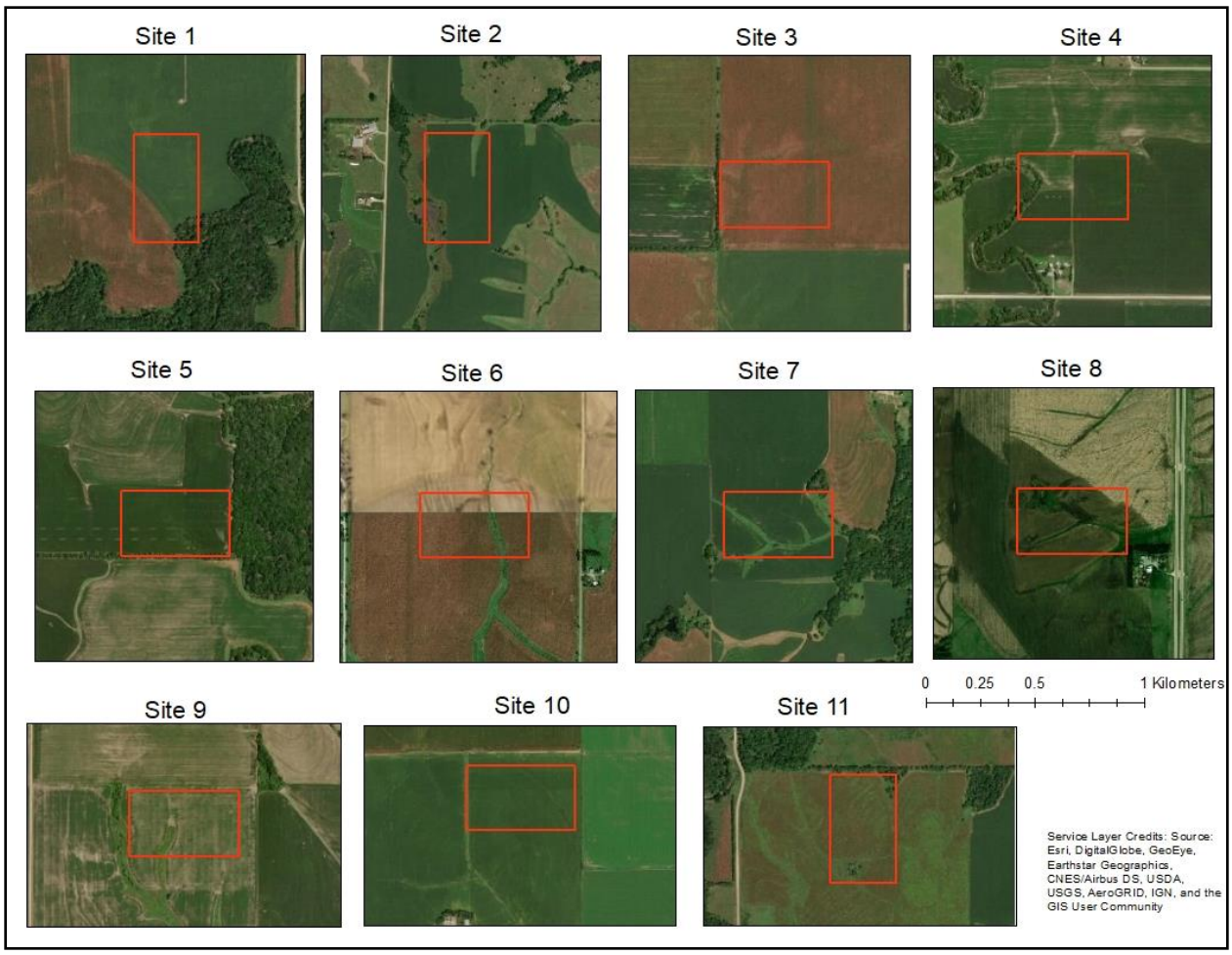

Figure 2.1. Agricultural sampling sites with border extents of acoustic detector grid placement in Gage and Lancaster counties, Nebraska to document summer movements of bats in crop fields. All sites were corn or soybean, except site 11, which was a restored tallgrass prairie.

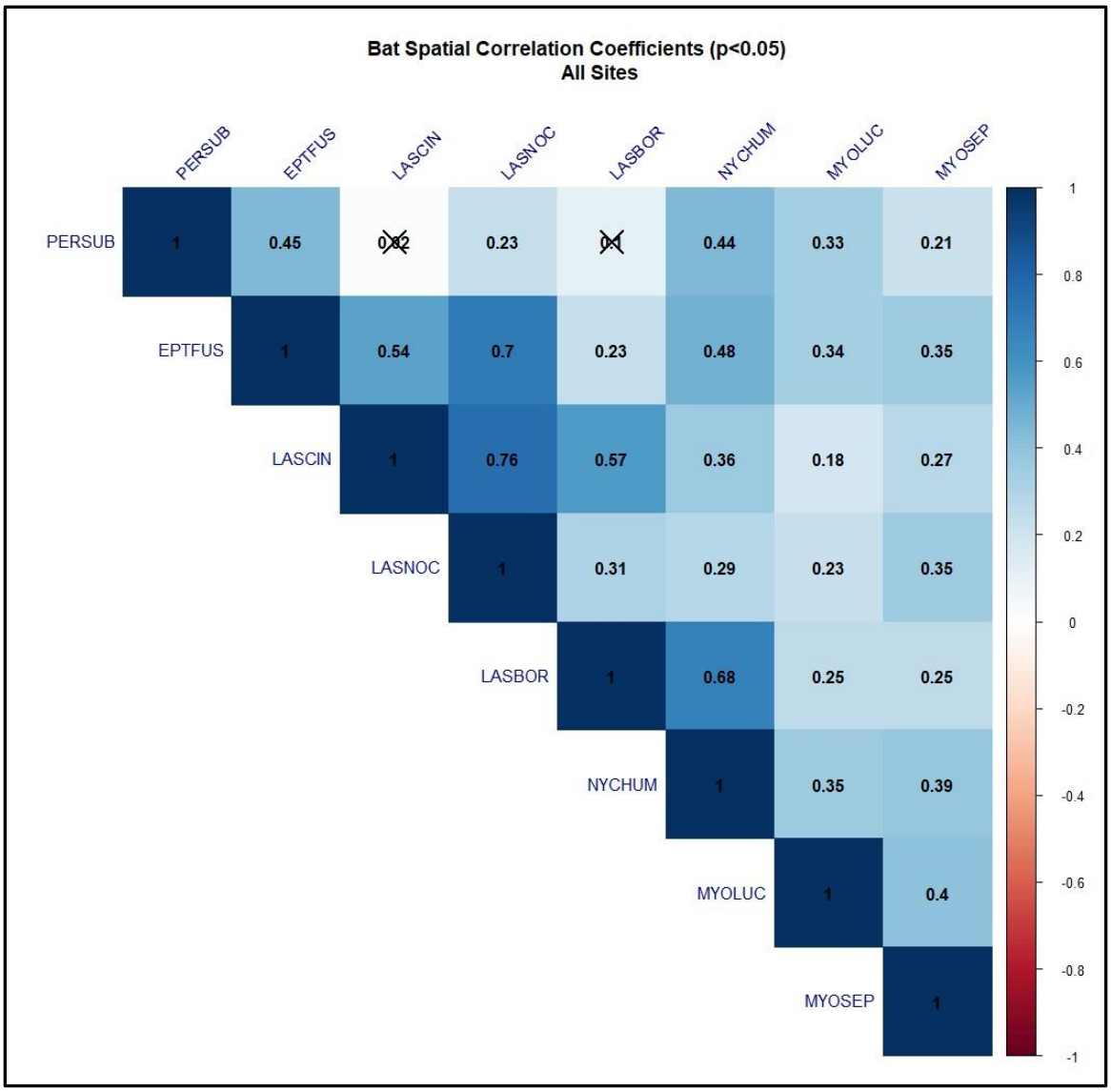

Figure 2.2. Spatial matrix of bat species in rural southeastern Nebraska for evidence of species spatial partitioning in an agricultural landscape across all sites Correlation coefficients (ρ) were calculated using Spearman rank correlation tests, and those relationships that were not statistically significant ($p<0.05$) are marked off. Darker blue values represent stronger positive relationships between species, while darker red values represent stronger negative relationships. Species are denoted by EPTFUS (big brown), LASBOR (eastern red), LASCIN (hoary), LASNOC (silver-haired), MYOLUC (little brown), MYOSEP (northern long-eared), NYCHUM (evening), and PERSUB (tricolored).

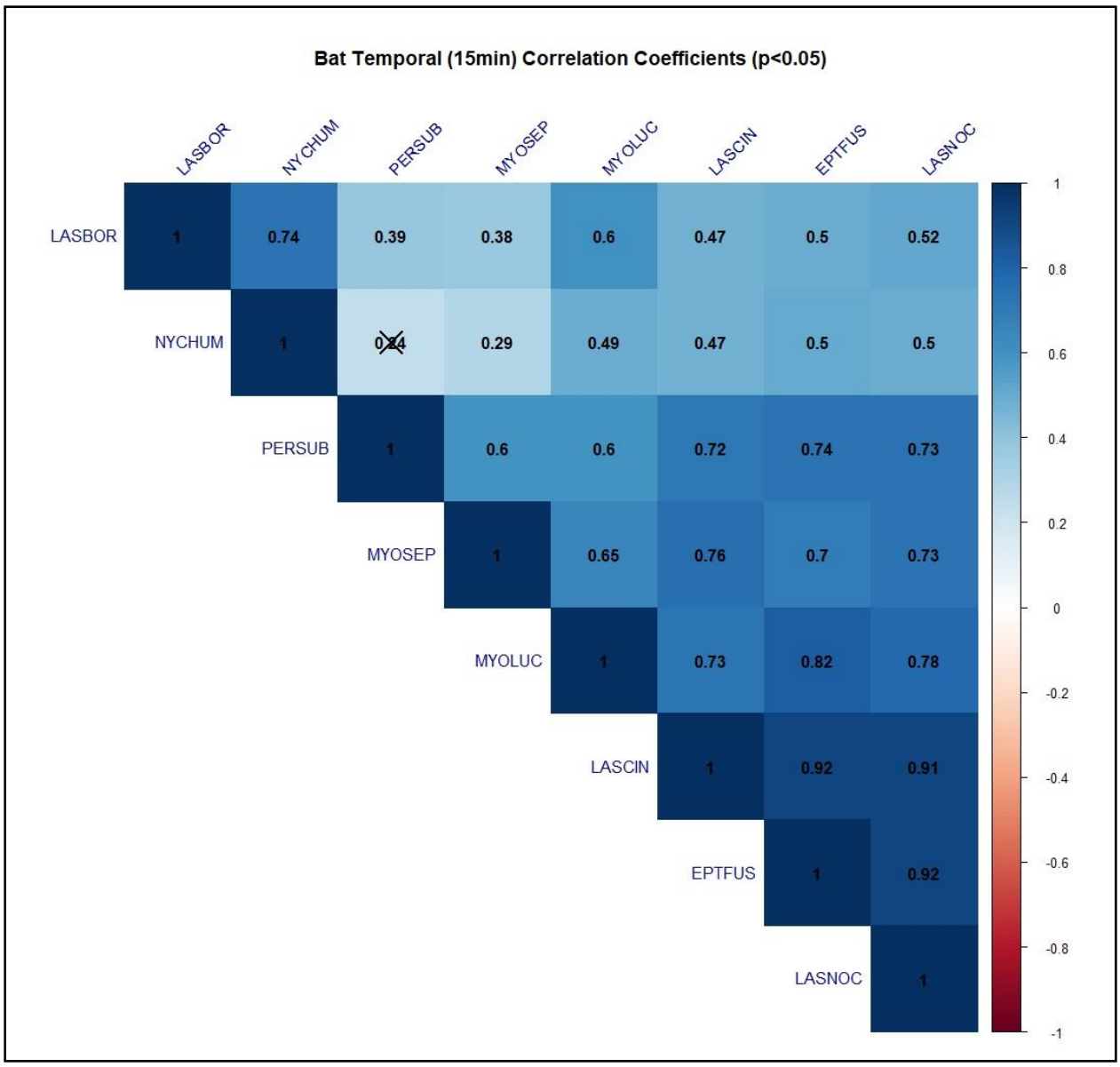

Figure 2.3. Temporal matrix of bat species from agricultural sites in southeastern Nebraska for evidence of species temporal partitioning in an agricultural landscape. Correlation coefficients (ρ) were calculated using Spearman rank correlation tests on 15 minute groupings, and those relationships that were not statistically significant ($p<0.05$) are marked off. Darker blue values represent stronger positive relationships between species, while darker red values represent stronger negative relationships. Species are denoted by EPTFUS (big brown), LASBOR (eastern red), LASCIN (hoary), LASNOC (silver-haired), MYOLUC (little brown), MYOSEP (northern long-eared), NYCHUM (evening), and PERSB (tricolored).

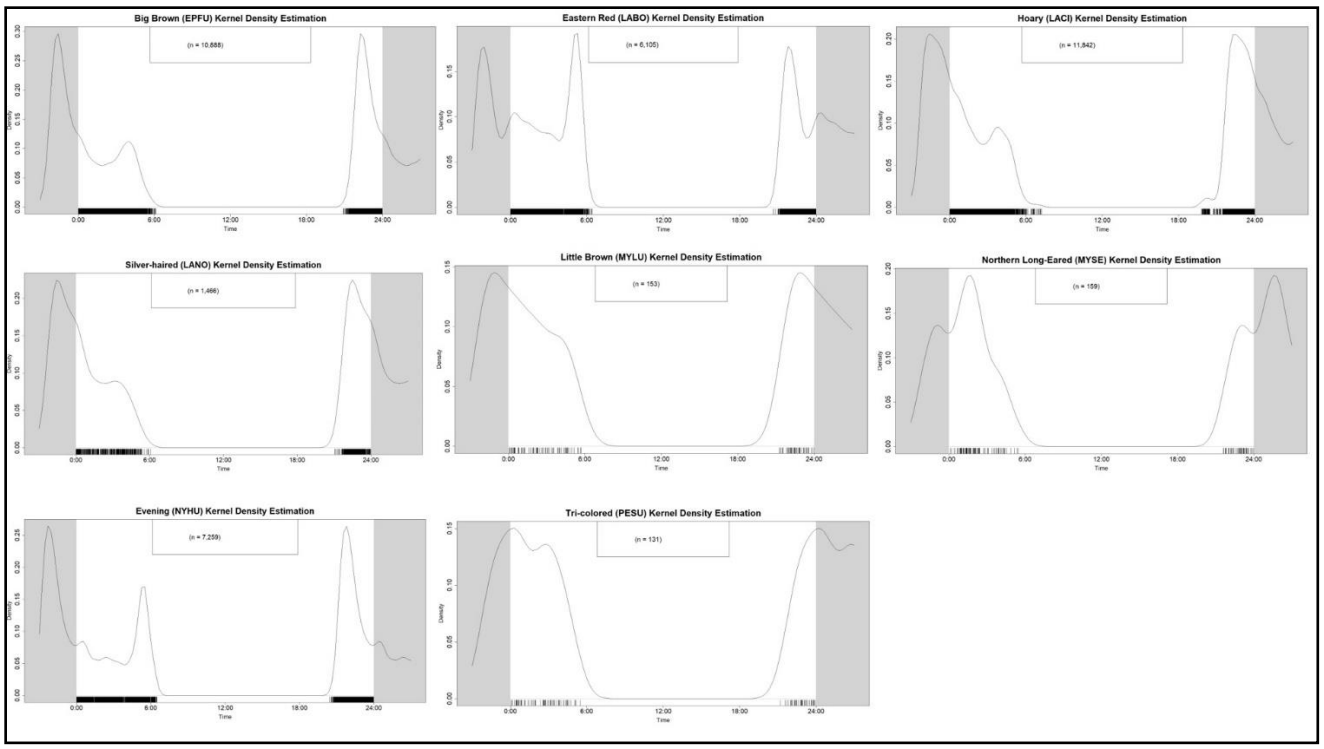

Figure 2.4. Kernel density estimations of bat temporal activity in crop fields across Gage and Lancaster Counties, Nebraska. Plots were produced using the R package *overlap* and by aggregating all acoustic time-stamped data. We used a smoothing factor of 1 since all species had a relatively high number of occurrences (Ridout & Linkie, 2009). Most species have two peaks, one after sunset and before sunrise, although eastern red and evening bats have an additional peak around midnight.

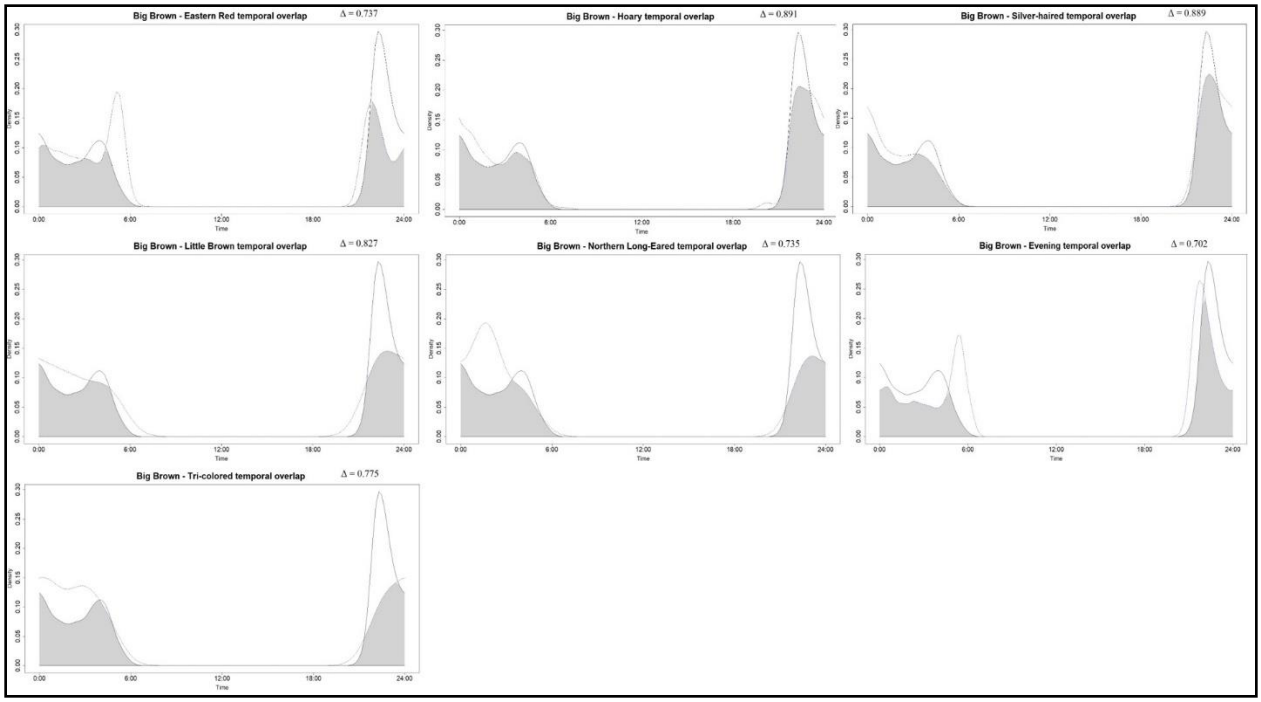

Figure 2.5. Temporal overlap between all bat species and the big brown bat (Eptesicus fuscus) in Nebraska crop fields for evidence of temporal partitioning. Plots and coefficients of overlap (Δ) were created using the R overlap package. All overlap coefficients were significant.

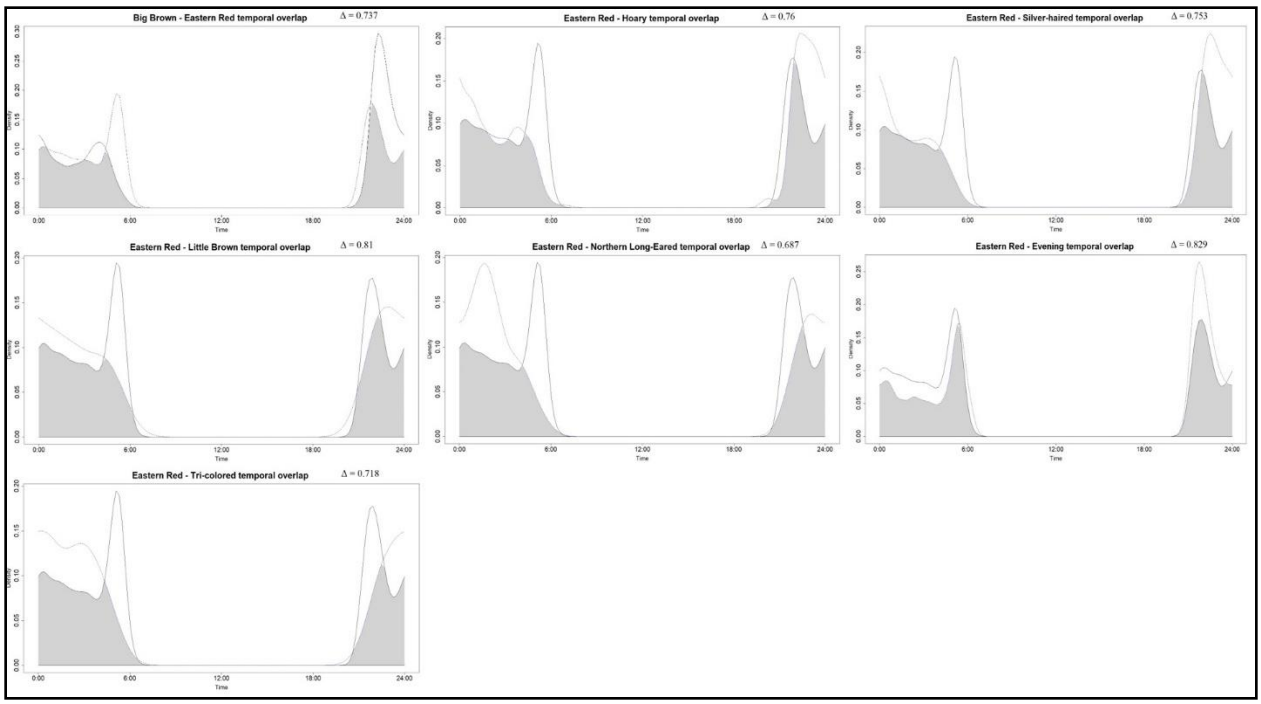

Figure 2.6. Temporal overlap between all bat species and the eastern red bat (Lasiurus borealis) in Nebraska crop fields for evidence of temporal partitioning. Plots and coefficients of overlap (Δ) were created using the R overlap package. All coefficients were significant.

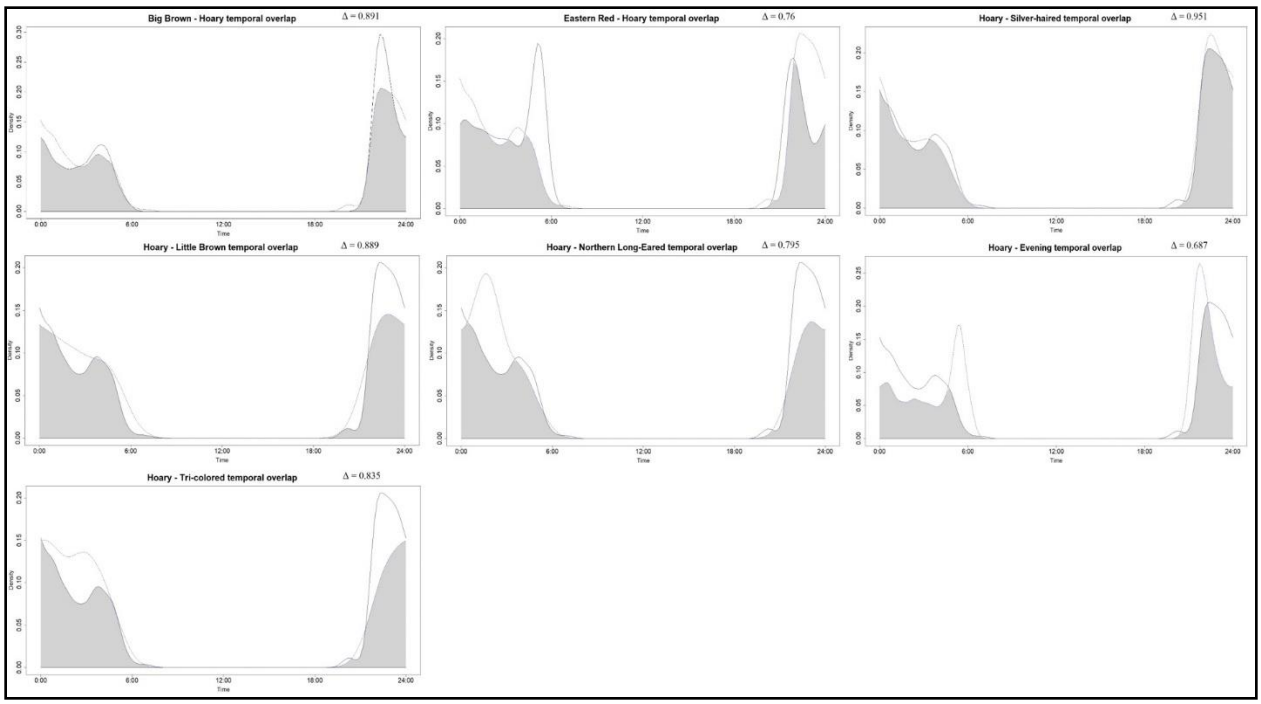

Figure 2.7. Temporal overlap between all bat species and the hoary bat (Lasiurus cinereus) in Nebraska crop fields for evidence of temporal partitioning. Plots and coefficients of overlap (Δ) were created using the R overlap package. All coefficients were significant.

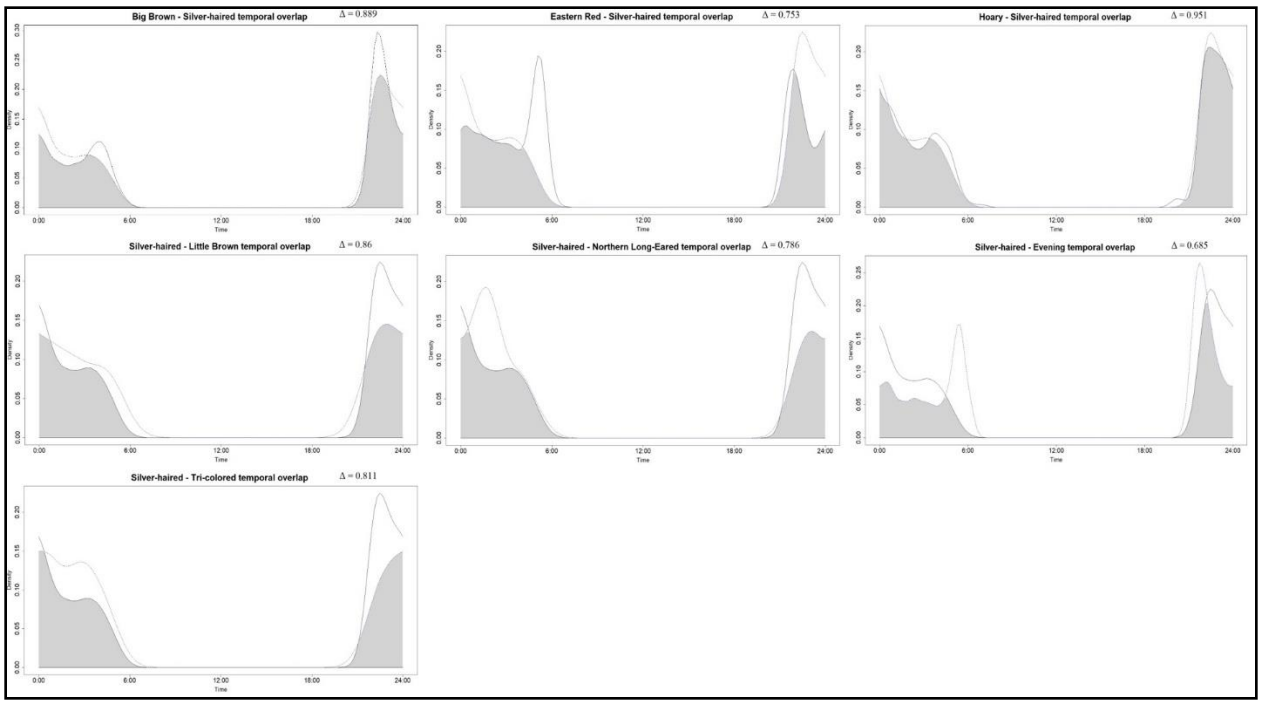

Figure 2.8. Temporal overlap between all bat species and the silver-haired bat (Lasionycteris noctivagans) in Nebraska crop fields for evidence of temporal partitioning. Plots and coefficients of overlap (Δ) were created using the R overlap package. All coefficients were significant.

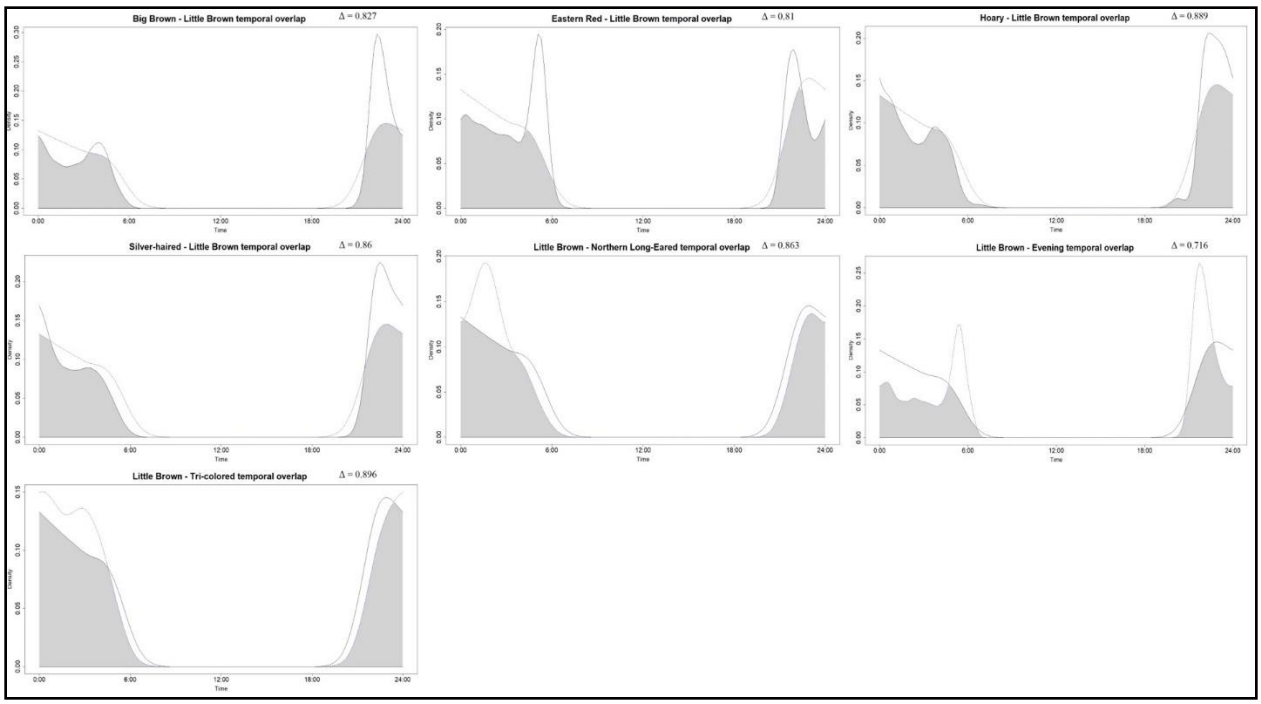

Figure 2.9. Temporal overlap between all bat species and the little brown bat (Myotis lucifugus) in Nebraska crop fields for evidence of temporal partitioning. Plots and coefficients of overlap (Δ) were created using the R overlap package. All coefficients were significant.

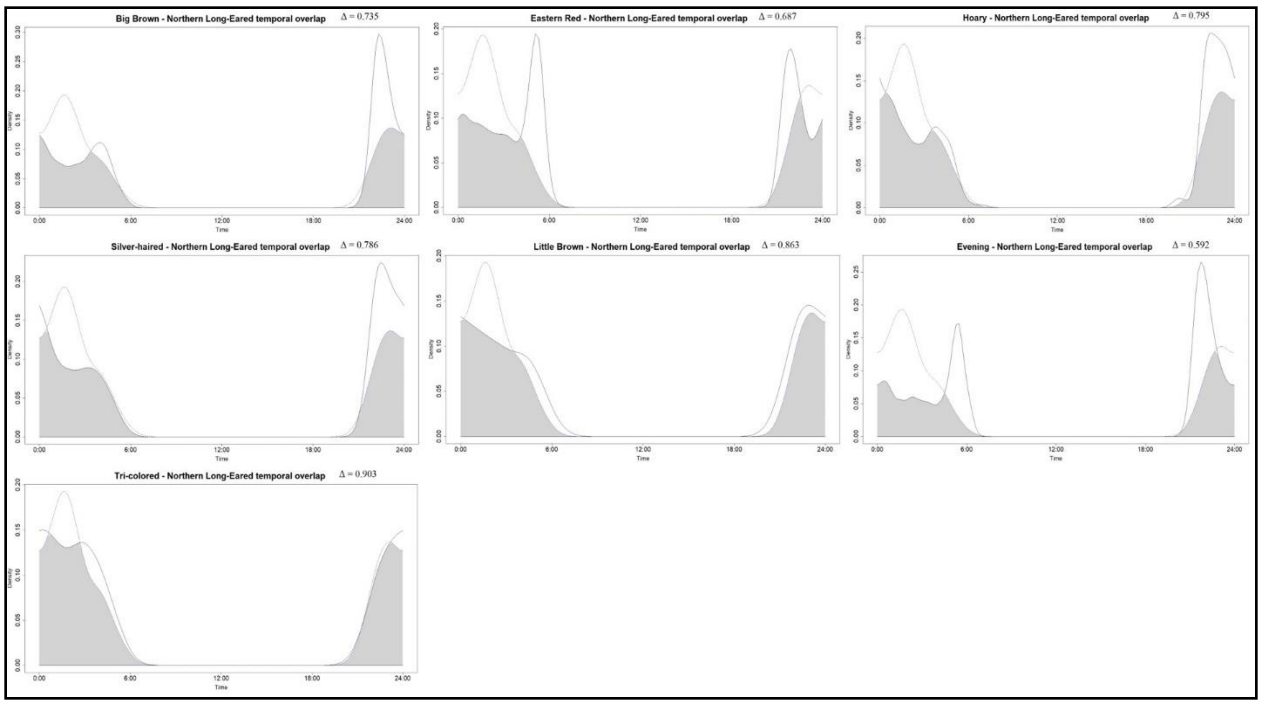

Figure 2.10. Temporal overlap between all bat species and the northern long-eared bat (Myotis septentrionalis) in Nebraska crop fields for evidence of temporal partitioning. Plots and coefficients of overlap (Δ) were created using the R overlap package. All coefficients were significant.

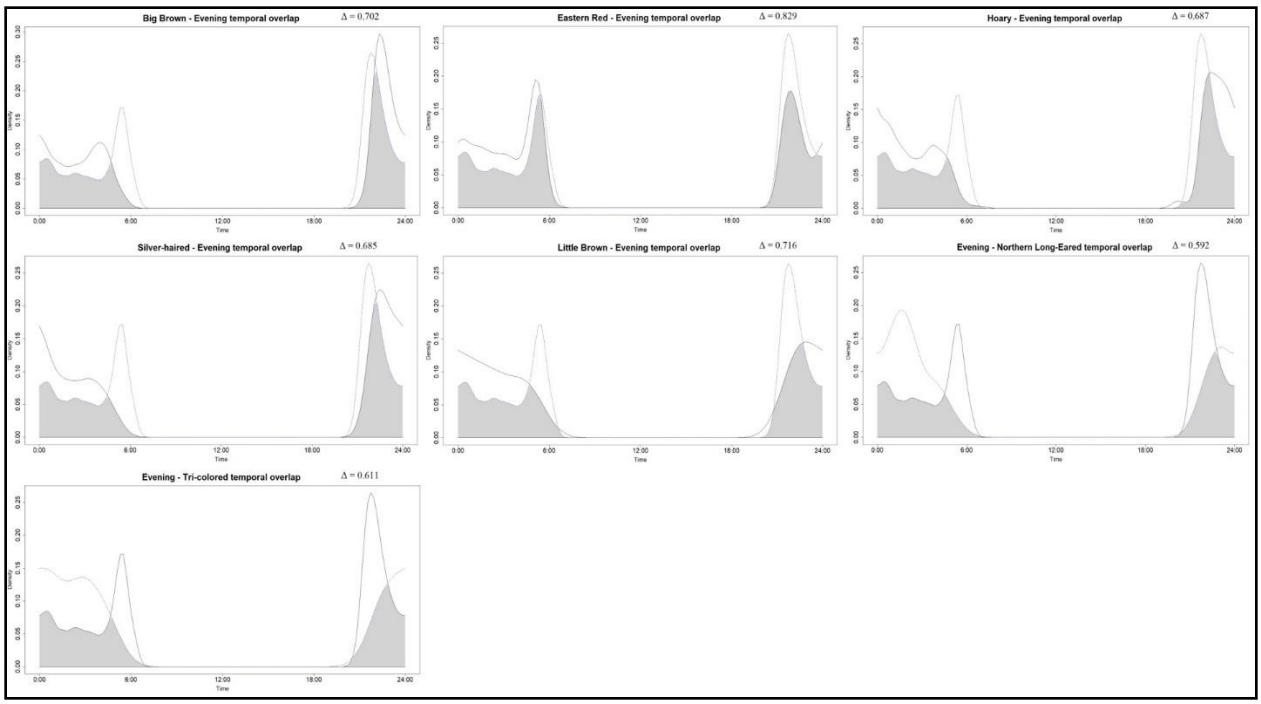

Figure 2.11. Temporal overlap between all bat species and the evening bat (Nycticeius humeralis) in Nebraska crop fields for evidence of temporal partitioning. Plots and coefficients of overlap (Δ) were created using the R overlap package. All coefficients were significant.

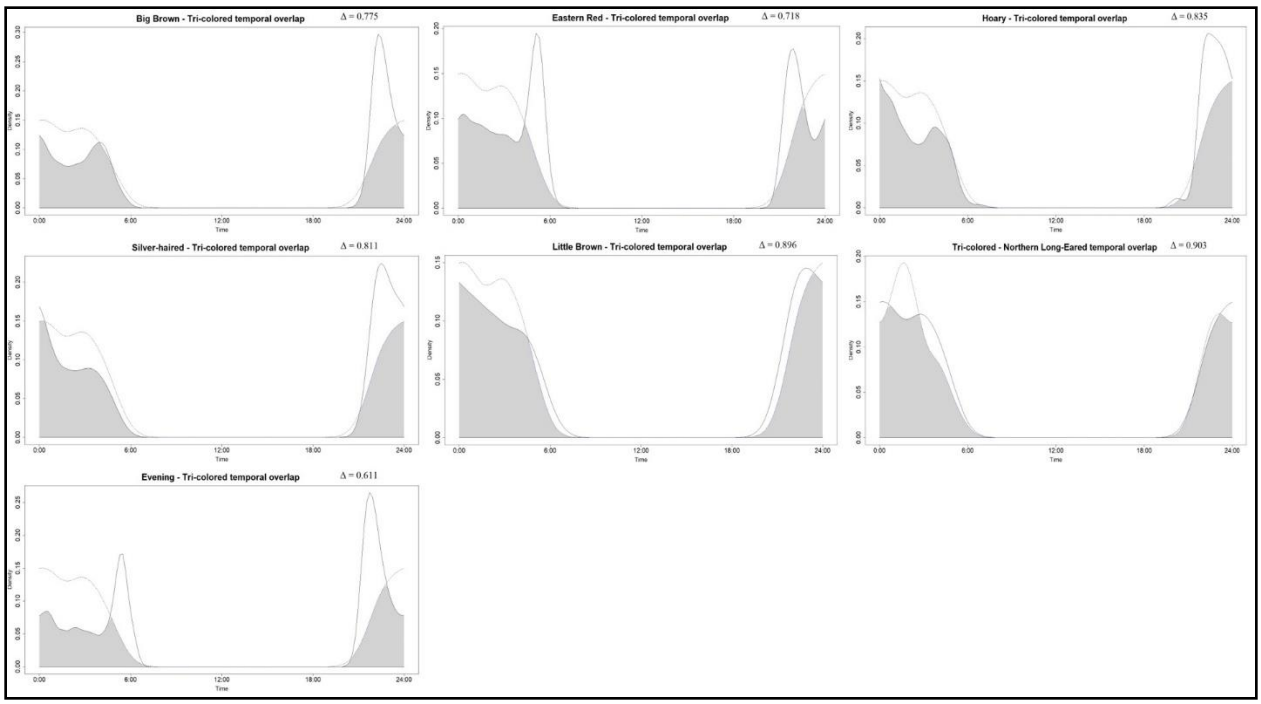

Figure 2.12. Temporal overlap between all bat species and the tricolored bat (Perimyotis subflavus) in Nebraska crop fields for evidence of temporal partitioning. Plots and coefficients of overlap (Δ) were created using the R overlap package. All coefficients were significant.

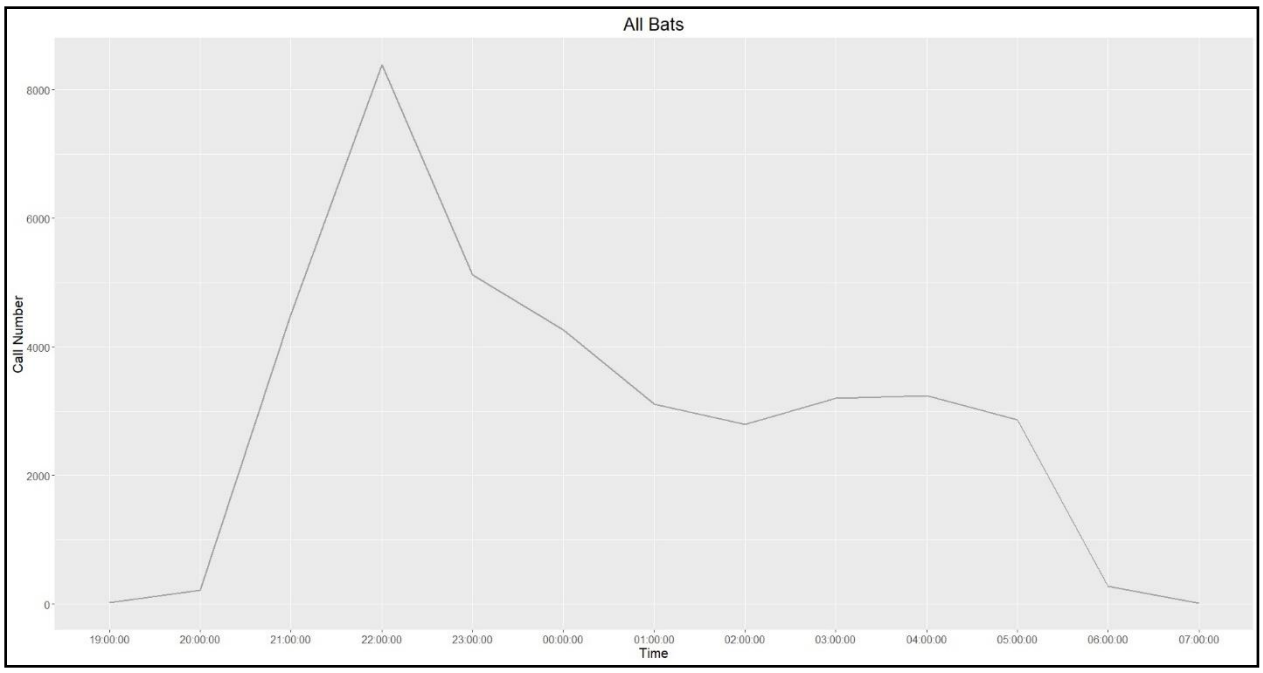

Figure 2.13. Collective temporal bat activity from agricultural sites in southeastern Nebraska to display peak times bats were active. Graph shows a bi-modal pattern, with the highest bat activity shortly after sunset at 22:00, followed by a lesser peak at around 4:00, shortly before sunrise.

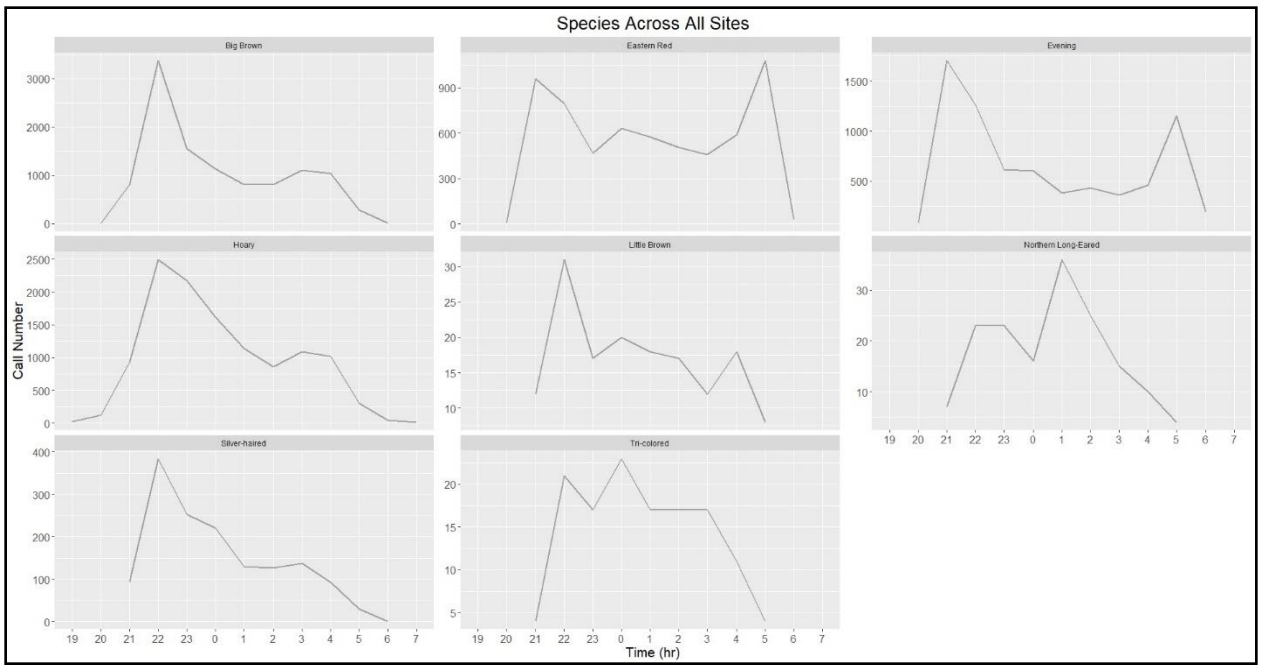

Figure 2.14. Collective species temporal activity patterns from agricultural sites in southeastern Nebraska to display peak times that bats were active relative to each other. Graphs show activity levels in hourly increments.

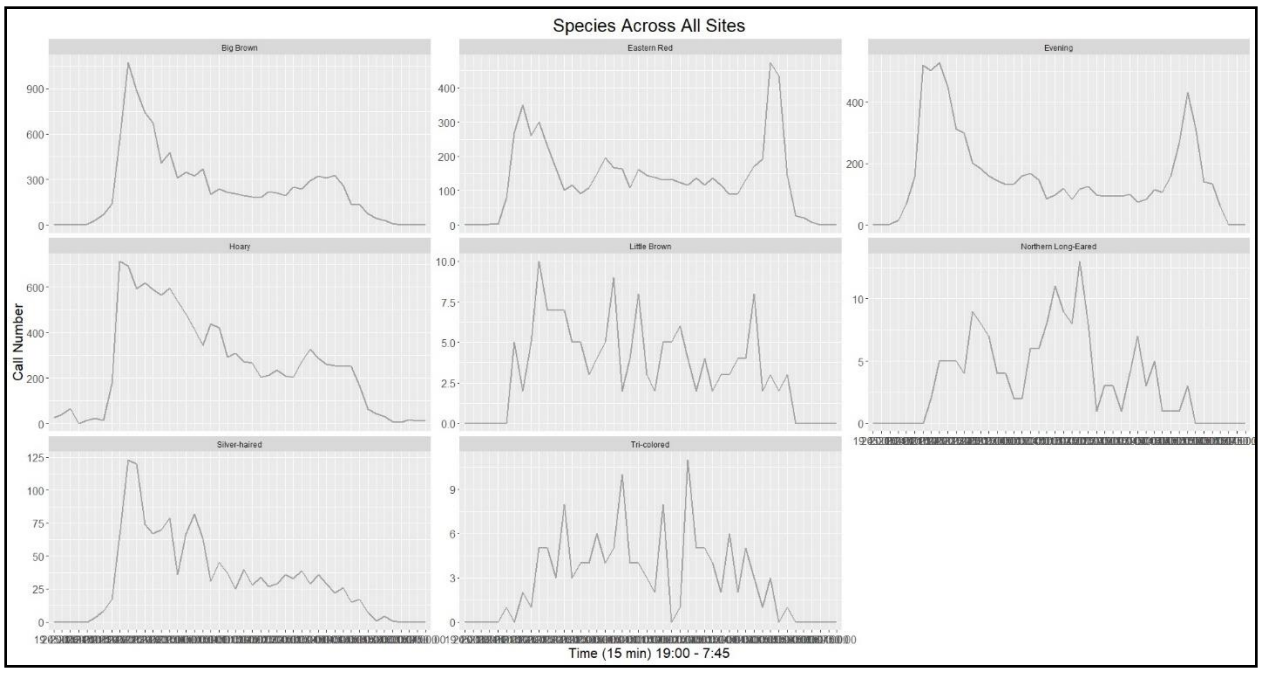

Figure 2.15. Collective species activity patterns from agricultural sites in southeastern Nebraska to display peak times that bats were active relative to each other. Graph shows activity levels from 19:00 – 7:45 in more detailed 15-minute increments.

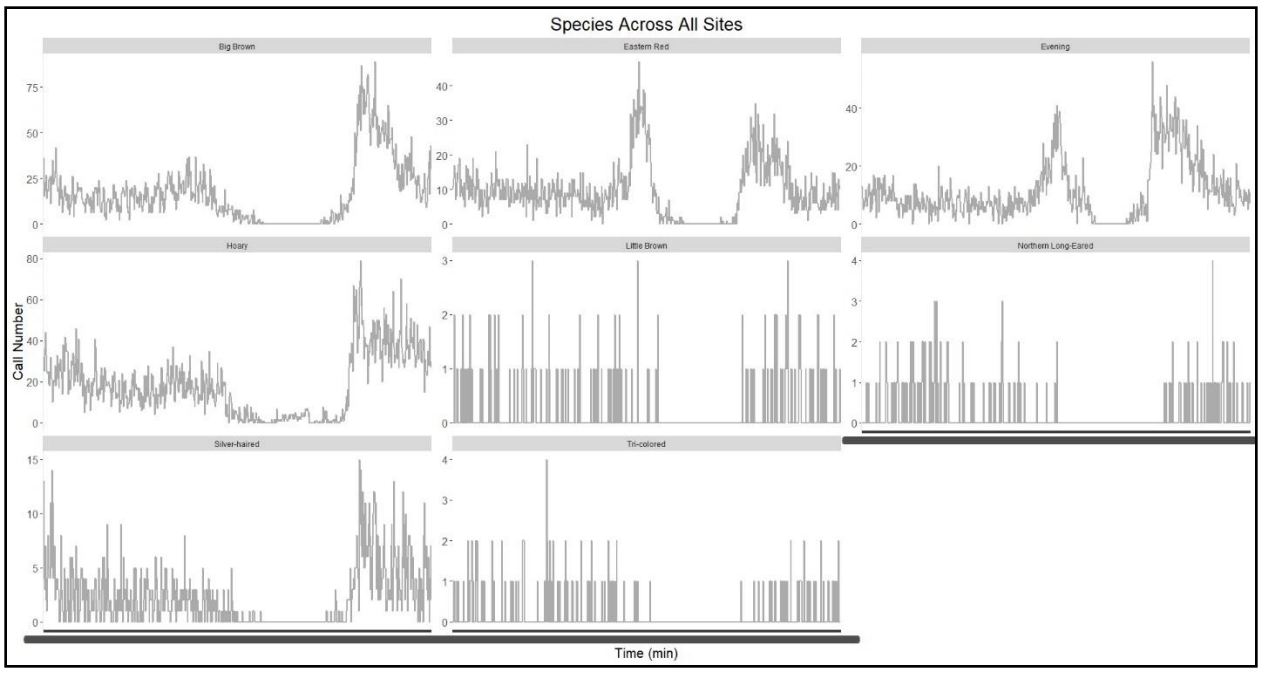

Figure 2.16. Collective species activity patterns from agricultural sites in southeastern Nebraska to display peak times that bats were active relative to each other. Graph shows activity levels by minute and illustrates the sporadic nature of little brown, northern long-eared, and tricolored bat activity, due to limited calls from these forest-associated species.

CHAPTER 3: ROOST BEHAVIOR OF A FEDERALLY THREATENED BAT (MYOTIS SEPTENTRIONALIS) IN AN AGRICULTURALLY DOMINATED LANDSCAPE

Abstract

Bats are important bio-indicators of ecosystem health and provide a number of ecosystem services. White-nose syndrome and habitat loss have led to the decline of many bat species in eastern North America, including the federally threatened northern long-eared bat, *Myotis septentrionalis*, reducing colonies by as much as 99 percent. White-nose syndrome was only recently found in Nebraska, which lies on the western extent of this species geographic range. To better understand how this forest-dependent species persists in an agriculturally dominated landscape amid a growing number of pressures, I investigated the roosting habits of this species at the Homestead National Monument of America, located in southeast Nebraska through netting and tracking efforts. Mist-netting activities took place on 8 nights in 2019 between August 16 and August 26, during which I caught 55 total bats of 5 species. With a permitted biologist, I trapped, tagged, and tracked five northern long-eared bats both outside and inside of the Monument. I only tracked two individuals to roosting sites, each using multiple roosts, with one selecting trees and snags two miles upstream of the park, and another using tree cavities and shadowbox fences in the park with other untagged northern long-eared bats. A few tagged individuals traversed the park between dusk and dawn. Results further confirm that at the distributional edge for this species, in an intensively managed agricultural landscape, wooded areas, riparian zones, and human-built structures are important resources for this imperiled species.

Introduction

Destruction of habitat is one of the primary causes for biodiversity loss (Tilman et al., 2001; Prescott et al., 2015). As humans seek to feed increasing populations, conversion of land for agriculture and intensification of current agricultural operations are likely to increase. Thus, it is important to understand how wildlife species exploit available habitats to allow for continued persistence in human modified landscapes.

The northern long-eared bat (*Myotis septentrionalis)* is a small, insectivorous species found throughout much of the eastern United States and Canada (Caceres & Barclay, 2000). Its relatively long ears are a key morphological feature that helps distinguish it from other *Myotis* species (Caceres & Barclay, 2000). These bats use a variety of echolocation calls that enable them to both glean prey from surfaces as well as capture airborne prey, allowing them to hunt in cluttered interior forest habitat, where they are often found (Patriquin & Barclay, 2003; Ratcliffe & Dawson, 2003; Henderson & Broders, 2008). *M. Septentrionalis* roost primarily in trees of a variety of types and stages, where females form maternity colonies and males tend to remain solitary (Foster & Kurta, 1999; Broders & Forbes, 2004; Carter & Feldhamer, 2005). This dependence on forest environments makes this species particularly vulnerable to habitat loss from deforestation. Due also to white-nose syndrome, an invasive fungal pathogen that starves hibernating bats by dissolving body tissue (Blehert et al., 2009; Frick et al., 2015), the species is no longer common throughout much of their range. The northern long-eared bat has been found to be particularly susceptible to white-nose syndrome (Frick et al., 2015) and it consequently was designated as threatened by the US Fish and Wildlife Service in 2015 (US Fish and Wildlife Service, 2015).

Nebraska lies on the western periphery of the species range and the fungus that causes white-nose syndrome has only recently been detected in Nebraska (White-nosesyndrome.org, 2019). The goal of this study is to describe the summer roosting habits of this species in the state's intensively farmed landscape at the Homestead National Monument of America preserve and surrounding areas. This landscape is unique in that northern long-eared bats are still abundant, this is the western limit of the species range, white-nose syndrome has not yet had an apparent impact on northern long-eared bat abundance, and most of the habitat available is due to afforestation following European colonization. The National Monument is located in southeast rural Nebraska, in an agricultural setting, and determining what features the bats utilize in the area will contribute to a better understanding of the habitat needs of this species in peril.

Methods

Study Area

Created in 1936, Homestead National Monument is located in Gage County in southeast Nebraska's glacial Drift Hill Region. The park covers roughly 195 acres, about two-thirds of which is restored native tallgrass prairie, and one-third mature lowland forest that straddles Cub Creek, which runs through the western portion of the park. The woodland consists mainly of cottonwood (*Populus deltoides*), hackberry (*Celtis* spp.), and oak *(Quercus* spp.). The restored prairie is primarily big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), and Indiangrass (*Sorgastrum nutans*). Private agricultural land use operations surround the monument. A prior study conducted in late spring of 2004 at the monument captured four northern long-eared bats over a two week period (Robbins, 2005).

Mist-netting and Telemetry

I obtained study protocol approvals (Project ID #1667) from both the University of Nebraska-Lincoln and the National Park Service Institutional Animal Care and Use Committees prior to sampling activities. I mist-netted for bats on eight nights between August 16 and August 24, with a focus on four different areas in the forested portion of the park. The first site was at the northern edge of the park, and comprised four nets along forest edges, park buildings, and below a bridge crossing the creek. The second site was at the southern edge of the park and consisted of two nets along a minimum maintenance trail and one at the forest edge. The third site was in the north central portion of the park, where three nets were on the walking trail, one was on the creek bank, and one over the creek. The fourth site was in the more limited access forest interior, where one net was also alongside, and another, over the creek. I sampled each of these sites for 1-3 nights over the course of the sampling effort (Fig. 3.1). I used nylon nets that ranged from 6 meters to 18 meters long, and assembled them single nets to triple-high stack setups, depending on the size of open flyway spaces in the forest canopy.

I began sampling each night at sunset and continued for at least 5 hours, unless severe or unfavorable weather systems developed. I checked nets at approximately 10 minute intervals and photographed the first of each species caught each night, as well as all northern long-eared bats, for documentation. I took basic morphological data on each individual captured, including weight, right forearm length, age, sex, reproductive condition, and wing damage index. Following USFWS protocol, a permitted biologist fitted each northern long-eared bat with a Holohil radio transmitter (Holohil Systems

Ltd., Carp, Ontario, Canada) with Perma-type adhesive (The Perma-Type Company Inc., Plainville, Connecticut, USA) to track movements and locate daytime roosts. I conducted telemetry search efforts primarily during daytime hours using Lotek wireless Biotracker units (Lotek Wireless, Newmarket, Ontario, Canada) attached to a five-element Yagi antenna, which I mounted on a truck and drove on roads within a 3 mile radius of the park. For bats I did not detect, I continued these search efforts at night after netting, as well as at sunset. I also mounted the antenna to a pole on site to detect tagged bats returning to the park during trapping periods. Tagged bats that were not found after one week I considered lost. At roost sites that were found, I recorded habitat features and an emergence survey conducted on the first night at each new roost, lasting from one half hour before sunset until one hour after sunset.

Results

Netting

Over 8 nights of netting, I caught 55 total bats across 5 different species, including big brown (*Eptesicus fuscus*), eastern red (*Lasiurus borealis*), hoary (*Lasiurus cinereus*), northern long-eared (*Myotis septentrionalis*), and evening (*Nycticeius humeralis*) bats. Evening bats were the most commonly caught species (28), followed by big brown (14), eastern red (7), northern long-eared (5), and hoary (1). Of the northern long-eared bats, all were young of the year, non-reproductive, and showed no signs of white-nose syndrome. Two of these I caught over the creek and three along forest trails, two of which I caught simultaneously in the same net. A permitted biologist placed transmitters on all five northern long-eared, and two fitted with forearm bands for identification purposes.

Tracking

The first northern long-eared was a female, and caught over the creek at the northern portion of the park at midnight. I never detected her with the telemetry equipment inside a 3-mile buffer radius around the park throughout the duration of the project.

The second northern long-eared was a male, and caught shortly after sunset simultaneously with another female northern long-eared in a net placed alongside a maintenance trail through the woods on the south side of the park. I tracked the male the following day to a large slippery elm (*Ulmus rubra*) on the bank of Cub Creek about two miles west of the monument (Fig. 3.2, Fig. 3.3, Fig. 3.4). After sunset the individual emerged with two other bats, and by midnight had made his way back to the park. I detected the female flying at sunset further west of the elm roost, and did not found her again until midnight, when she had also returned to the monument. I did not encounter this female with the telemetry equipment throughout the remainder of the project. I found the male the second day under a raised slab of bark on a downed limb at about two meters above the ground just east of the previous roost site. This limb was charred by fire and located in a burned clearing between a corn field and the creek, along with other large downed burned trees and stumps (Fig. 3.2, Fig. 3.3, Fig. 3.5, Fig. 3.6). After emergence, I found this male traveling in the roost area at 2:30am, and roosting the following day in the same area along the creek, but did not track down to a specific roost. I did not detect the male for the remainder of the project.

The fourth northern long-eared bat was a female caught just after midnight over the creek near the parking lot. In addition to tagging, I also attached a forearm band,

however I never detected this bat with the telemetry equipment inside a 3-mile buffer radius around the park throughout the remainder of the project.

The fifth northern long-eared bat was also a female, caught shortly after sunset over a mowed trail in the northern wooded section of the park. I banded this individual as well, and detected her traveling in and around the monument that night until she roosted beneath the trimmed top of a shadow box fence on the western edge of the park (Fig. 3.7, Fig. 3.8). Following emergence, I found her again flying in and around the park until she roosted in the same section of fence, only this time with another non-banded and untagged northern long-eared bat (Fig. 3.9). The next day, I found her in a small cavity near the base of a young hackberry (*Celtis occidentalis*) near her capture site along the forest loop trail (Fig. 3.7, Fig. 3.10). She emerged with one other bat. The following day, she was in a smaller shadow box fence on the south side of the park housing complex, and I subsequently tracked her to a large cottonwood (*Populus deltoides*) in the center of the prairie portion of the park the day after (Fig. 3.7, Fig. 3.11). However, I did not detect an emergence, and a banded bat was found in the same western shadow box fence that night, leading me to believe she had dropped the transmitter in the cottonwood. The transmitter remained in the same cottonwood until tracking concluded on September 2nd. The banded bat was not in the fence the following day however, but a non-banded and untagged northern long-eared bat was. The banded individual returned to the fence the following two days, and I did not search the fence again until September 2nd, when she was again utilizing it. Park Service staff found a non-banded northern long-eared bat in the fence when they searched it eight days later.

Discussion

Acoustic results from other studies in the surrounding area (see chapter 1 and 2) suggested eight species to be present at the park, and of these five I actually caught. Evening bats were the most abundant species, followed by big brown, eastern red, northern long-eared, and hoary (Table 3.1). A considerable number of individuals caught were young of the year, and had matured rapidly enough to be considered adults at the time of capture. All five northern long-eared caught fit into this category, and none showed any signs of white-nose syndrome, as they likely had not yet had to hibernate. The hoary capture was unexpected, as it occurred in a woody area, and they are usually seldom caught or seen. No little brown, silver-haired, or tricolored bats were caught, although presence was suggested by acoustic data. Tricolored presence was questionable even from the acoustics collected. Robbins (2005) also caught primarily evening (12) but fewer northern long-eared bats (4), the majority of which were pregnant, and no other species.

Of the five northern long-eared bats caught, three were caught alongside woodland trails, and two over the creek itself. Interestingly the woodland captures of this species all occurred before 20:00, suggesting these bats likely roosted close by. However, both creek captures happened just before or after midnight, indicating these bats could be using the waterway to facilitate quicker and less exposed movement at later night hours. Only three tagged bats were heard with the telemetry unit, and of these, two tracked to actual roosts. It's likely the two others flew beyond the 3-mile buffer radius after tagging, or were roosting inside one of the many barns or sheds in the area. However, neither was heard even with telemetry gear positioned at sunset, when bats

emerge and the unobstructed transmitter signal can carry further. On the instances the other three were tracked during night hours, they appeared to be traveling in the monument and along the riparian corridor to or from external roost sites, two of which were located about 2 miles away upstream. The third northern long-eared bat was heard at sunset even further upstream from the park, suggesting these bats are capable of flying considerable distances over the course of a single night.

The two bats I tracked down to roosts utilized a variety of different woody structures, most of which were in close proximity to the creek. These spanned from large cottonwood and elm trees 25 – 30 meters above the ground, to raised bark on a burnt snag and a small hollow near the base of a young hackberry, each only about 2 meters above the ground. Curiously, the last female northern long-eared appeared to rely heavily on a shadow box fence surrounding the park housing complex, roosting in the cavity beneath the trimmed top. On one occasion, she was alongside another unidentified northern long-eared bat (Fig. 3.9), and while it is impossible to say if this individual was the same non-banded northern long-eared found in the fence multiple times, or was in fact different bats, these fences appeared to be an important man-made roosting feature for this species. Interestingly enough, I did not encounter any other bat species using this fence over the course of the project. Since this female northern long-eared spent considerable night hours in the park, and all tracked bats were heard in the park at night on at least one occasion, it is likely these individuals were using this area for foraging purposes in addition to travel and roosting.

This study demonstrated that northern long-eared bats are using Homestead National Monument to roost, travel, and likely forage, and sheds more light on the

movements and opportunistic roosting habits of this threatened species at the western edge of its range. The success rate at which young northern long-eared bats were caught mirrors that of the 2004 park study, indicating this species is persisting in this environment, despite the imminent arrival of white-nose syndrome to the area, as well as intensive farming. The five different species of bats caught throughout the study suggests that the park offers valuable habitat for most of the species that occur in the area, and should be maintained in order to do so into the future. The forested riparian area that runs through the park and surrounding agricultural areas likely serves as a corridor to facilitate bat presence and movement in a historically treeless landscape.

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Tables and Figures

Table 3.1. Total bat captures by species over eight nights from August 16 – August 24 at Homestead National Monument.

Species	Common Name	Number
EPFU	Big Brown	14
LABO	Eastern Red	7
LACI	Hoary	1
MYSE	Northern Long-Eared	5
NYHU	Evening	28

Table 3.2. Morphological capture data on individual northern long-eared bats caught at Homestead National Monument.

Date	Species	Age	Sex	Repro.	Wt. (g)	RFA (mm)	Wing Index
8-16	MYSE 1	Ad	F	NR	8	37	0
8-17	MYSE 2	Ad	M	NR	8	34	0
8-17	MYSE 3	Ad	F	NR	5	34	0
8-19	MYSE 4	Ad	F	NR	7	35	0
8-21	MYSE 5	Ad	F	NR	6	36.5	0

Table 3.3. Roost site descriptions for tracked northern long-eared bats caught at Homestead National Monument. An unbanded and untagged northern was documented roosting in the same fences three times over the course of the project.

Date	Bat	Roost Num.	Species	Tree Ht. (m)	Roost Type	Roost Ht. (m)
18-August	MYSE #2	1	Slippery Elm	45	Unknown	25
19-August	MYSE #2	2	Burned Snag	1.75	Bark	1.75
22-August	MYSE #5	1	Fence	1.82	Hollow	1.74
23-August	MYSE #5	2	Fence	1.82	Hollow	1.74
24-August	MYSE #5	3	Hackberry	6	Hollow	1
25-August	MYSE #5	4	Fence	1.67	Hollow	1.61
26-August	MYSE #5	5	Cottonwood/Fence	30	Unknown/Hollow	12
28-August	MYSE #5	6	Fence	1.82	Hollow	1.61
29-August	MYSE #5	7	Fence	1.82	Hollow	1.74
2-Sept	MYSE #5	8	Fence	1.82	Hollow	1.74

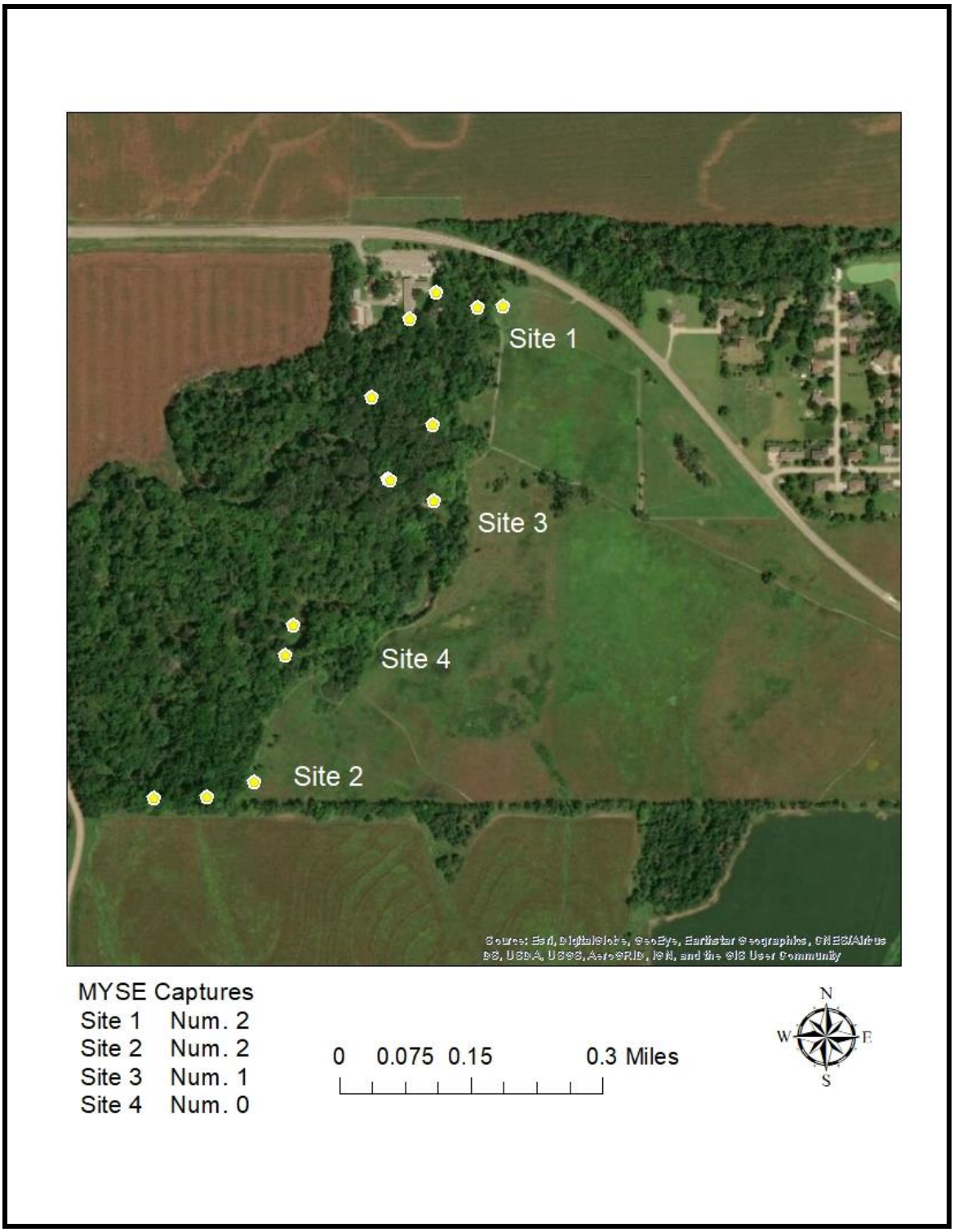


Figure 3.1. Mist-netting setup locations in Homestead National Monument over the course of the project. Each net was open from 1 – 2 nights each, with 2 – 4 open at a time.

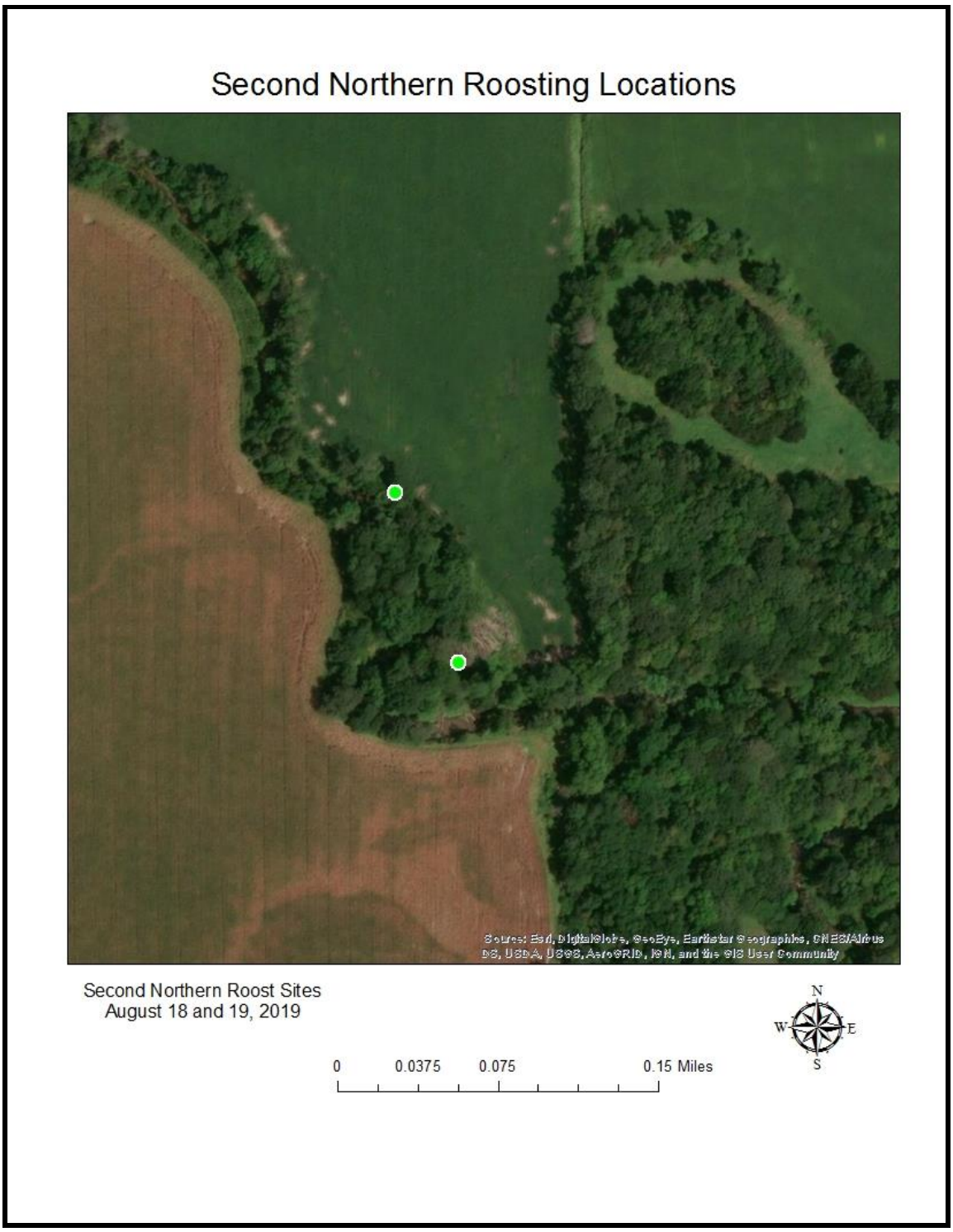


Figure 3.2. Roost tree locations used by the second tagged Northern Long-Eared (male). The first roost (*Ulmus rubra*) is located at the upper left, and the roost utilized the following day is on the lower right (burnt snag). Both roosts were located near the riparian corridor and at the edge of large corn fields.

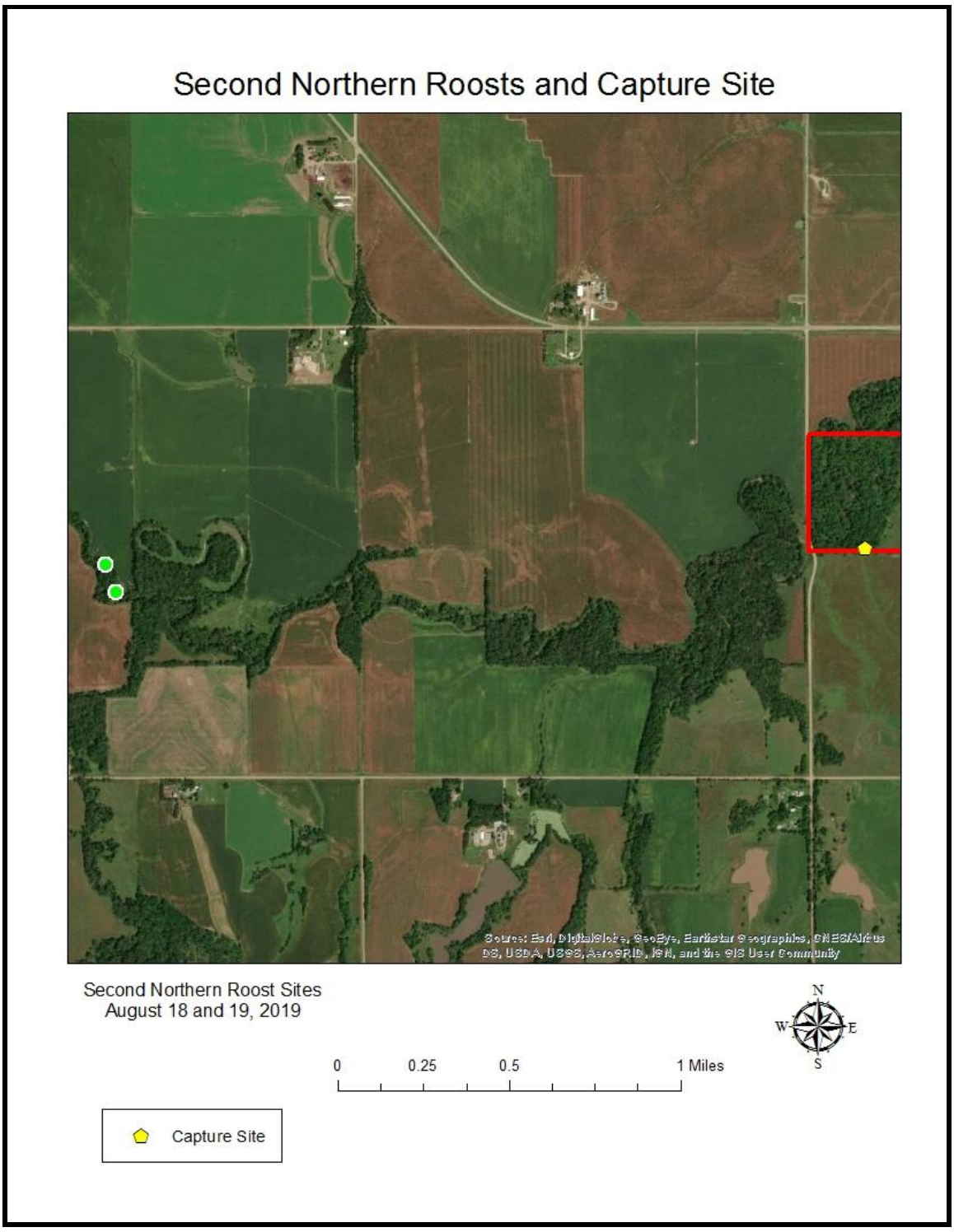


Figure 3.3. Locations of roost trees used by the second tagged Northern Long-Eared (male). Roosts were approximately 2 miles west of capture site. Documented flight activities appeared to occur primarily between the capture and roost sites along the riparian corridor.

Figure 3.4. Slippery Elm (*Ulmus rubra*), the first roost used by the second northern (male) following capture. This tree was approximately 45m tall with a dbh of 74.84cm. The actual roosting bat was estimated to be about 25m up the tree, and emerged with two other bats. (P.C. Christopher Fill)

Figure 3.5. Second roost used by the second northern (male) on August 19. Roost was located under a raised section of bark just to the right to the highest section of the burnt snag, about 1.75m tall. This limb was located in a burned brush clearing between Cub Creek and a large corn field. (P.C. Christopher Fill)

Figure 3.6. Second northern (male) utilizing roost in burned snag on August 19. Transmitter antenna visible. (P.C. Christopher Fill)

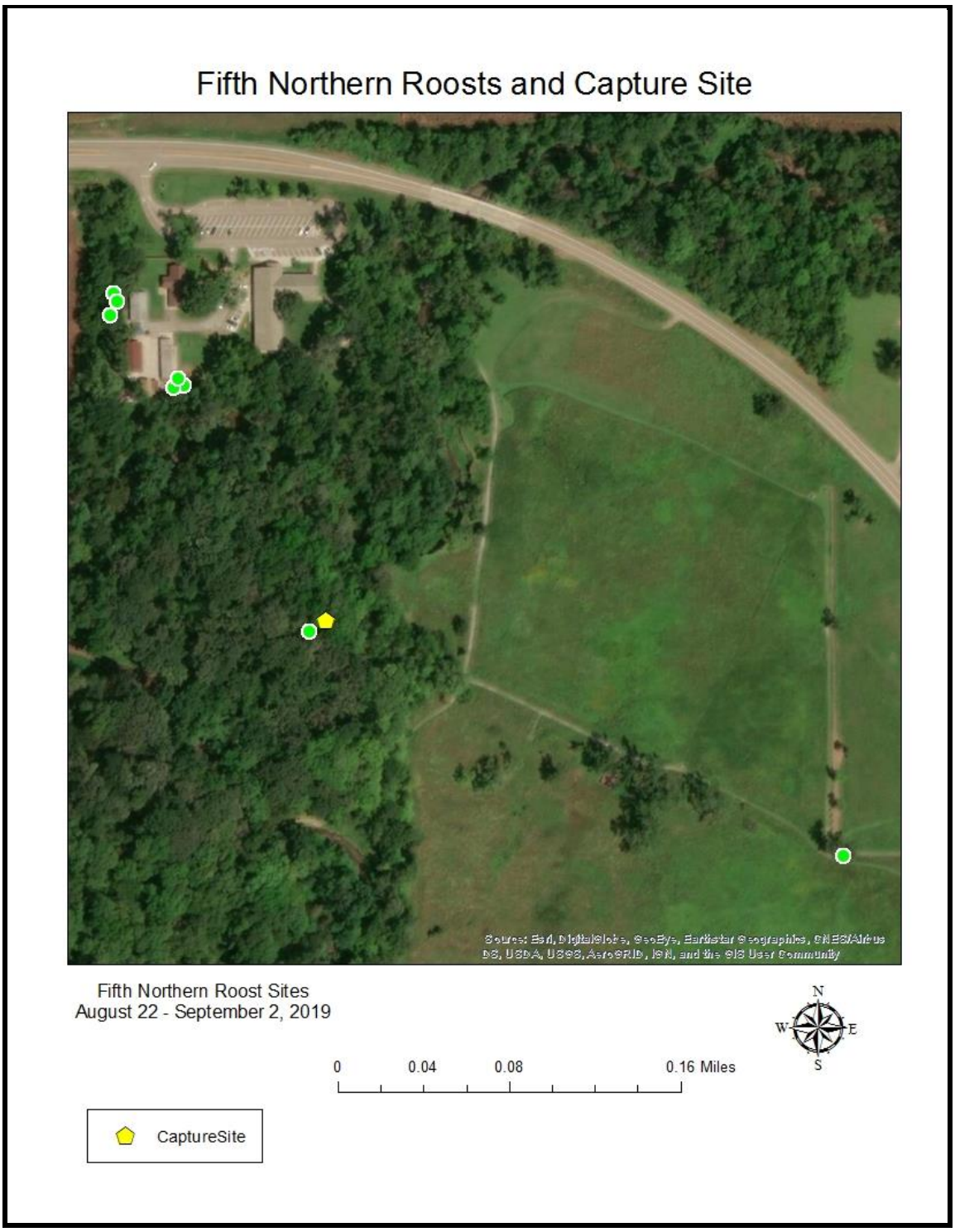


Figure 3.7. Roost locations used by the fifth tagged Northern Long-Eared (female) in Homestead National Monument. The female occupied multiple roosts in a fence by park housing in the upper left map corner. Trees utilized included a Hackberry by the capture site, and a Cottonwood. Documented flight activities appeared to occur primarily in and around the park.

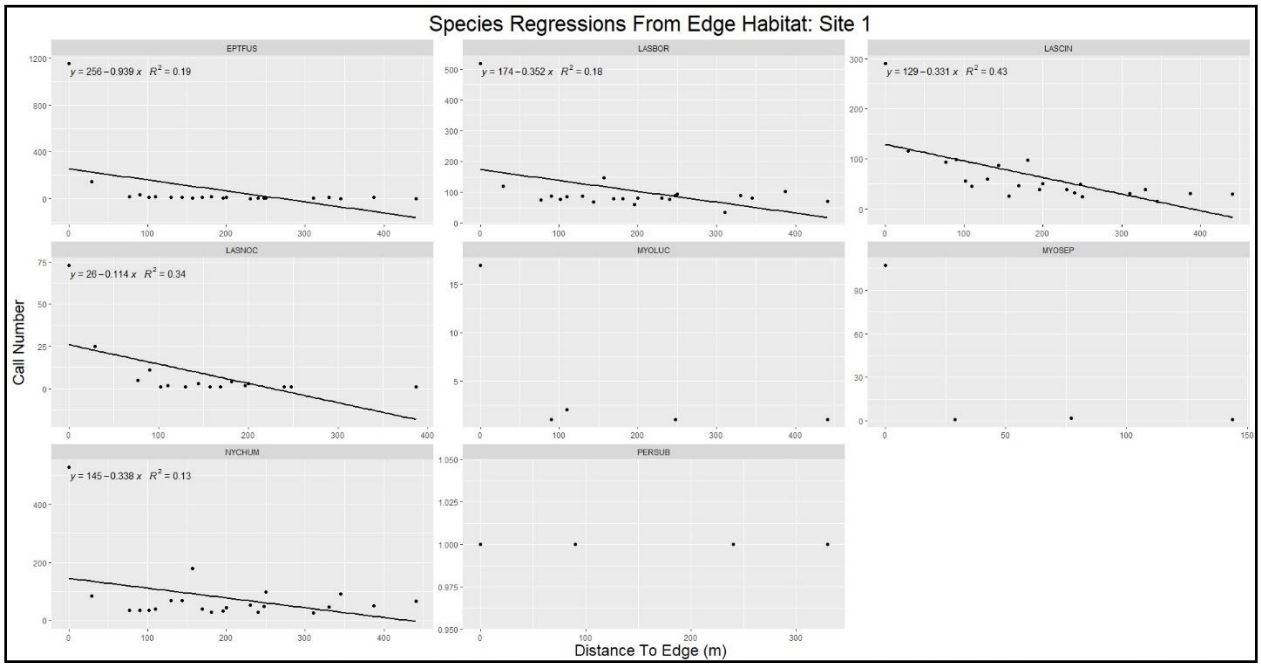
Figure 3.8. Shadow box fence utilized by the fifth northern (female) on six different occasions. Roost was located in the gaps formed under the lip of the trimmed top over alternating panels. The fence was located on the western edge of the park housing complex. This northern was also found once in a shorter identical fence on the southern edge of the housing complex. (P.C. Christopher Fill)

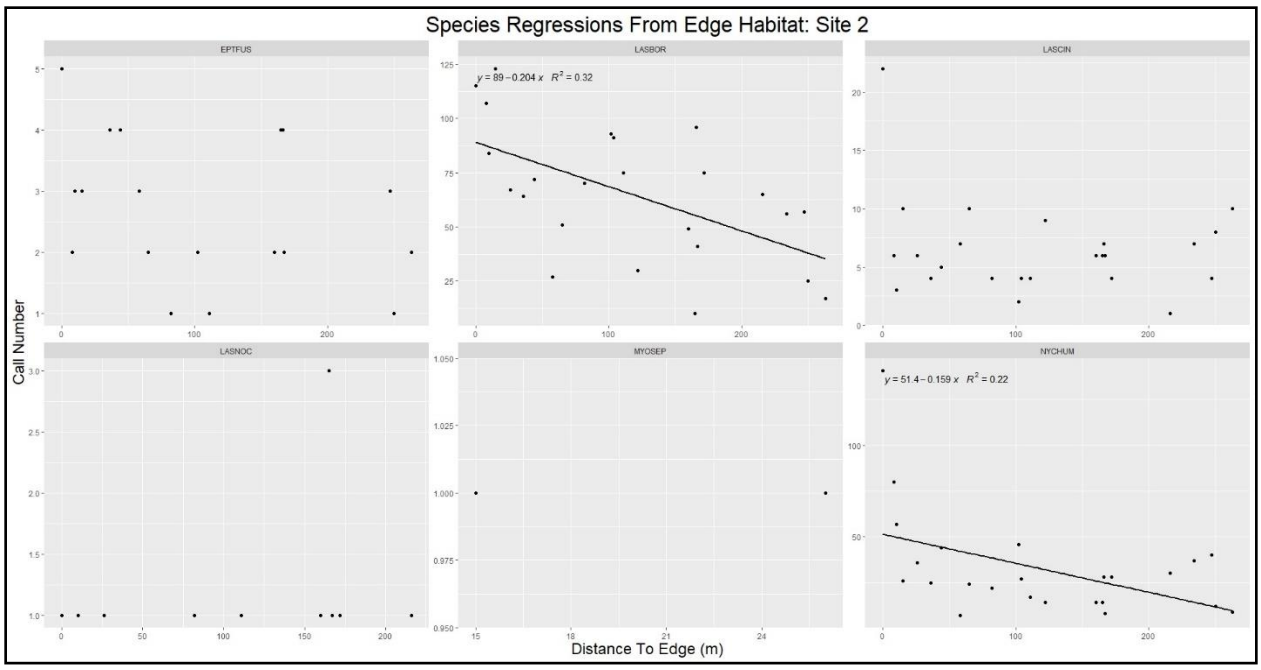
Figure 3.9. Fifth northern (female) utilizing fence cavity at Homestead as a daytime roost on the second day of tracking, August 23. This tracked individual was found with another unidentified northern on this one occasion. A solo untagged northern was found in the same fences on two other occasions. (P.C. Benjamin Hale)

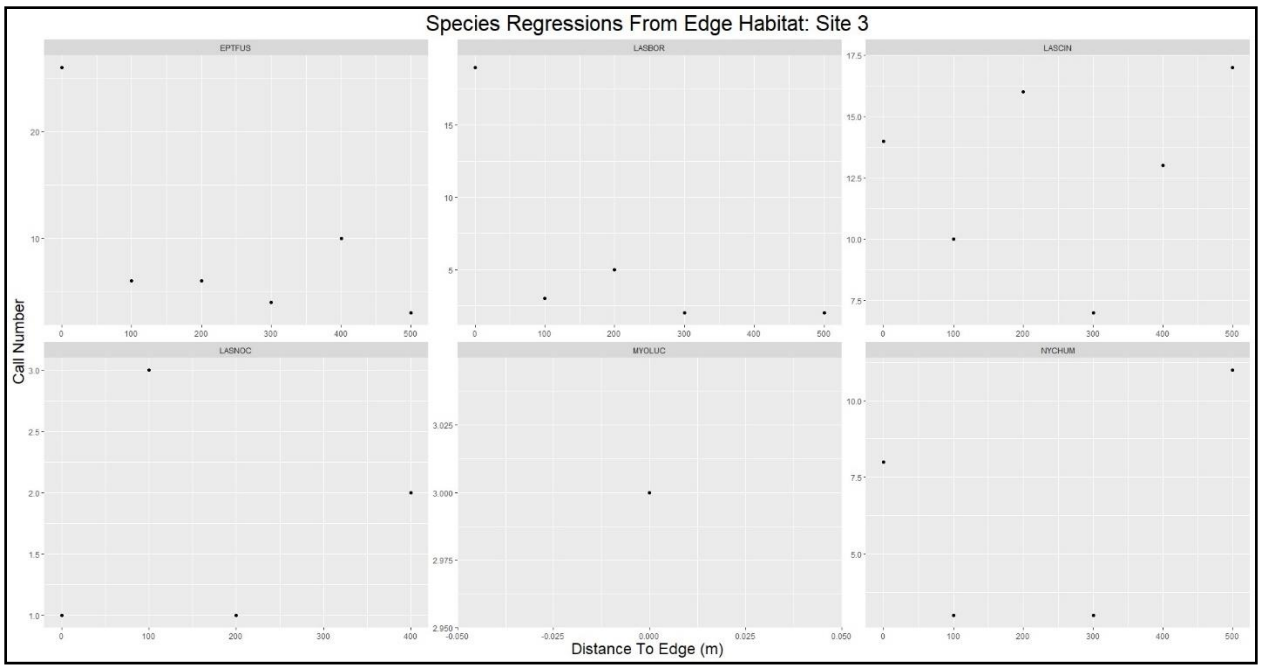
Figure 3.10. Cavity at the base of a young Hackberry (Celtis occidentalis) that was used by the fifth northern (female) on August 24 in Homestead National Monument. The roost was approximately 1 meter off the ground and next to the capture site. This tree was approximately 6m tall with a dbh of 7cm. The northern emerged with one other bat. (P.C. Benjamin Hale)

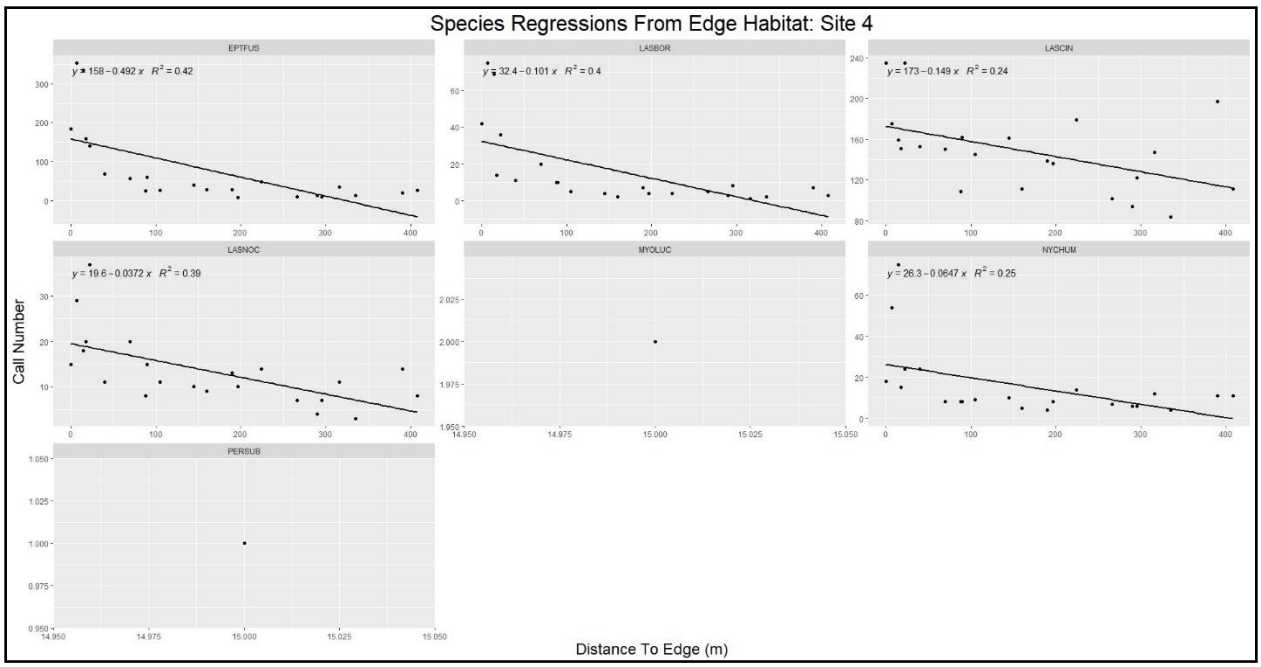
Figure 3.11. Eastern Cottonwood (Populus deltoides) in which the fifth northern lost her transmitter overnight on August 26 in Homestead National Monument. The transmitter was estimated to be about 12 m up into the approximately 30 m tree, which had a dbh of 65.29cm. (P.C. Christopher Fill)

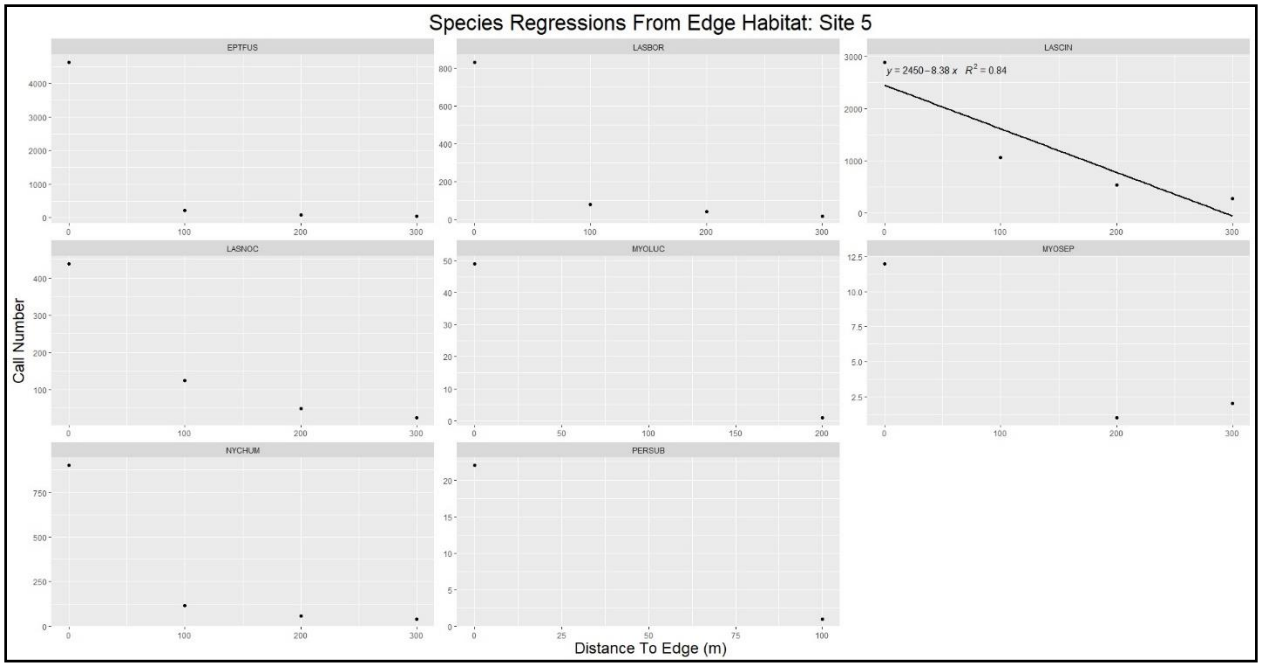
APPENDIX A. SITE SPECIFIC SPATIAL REGRESSION RESULTS FROM EACH FIELD EDGE, WITH R^2 FOR EACH SPECIES WITH SIGNIFICANT P-VALUES ($p < 0.05$).

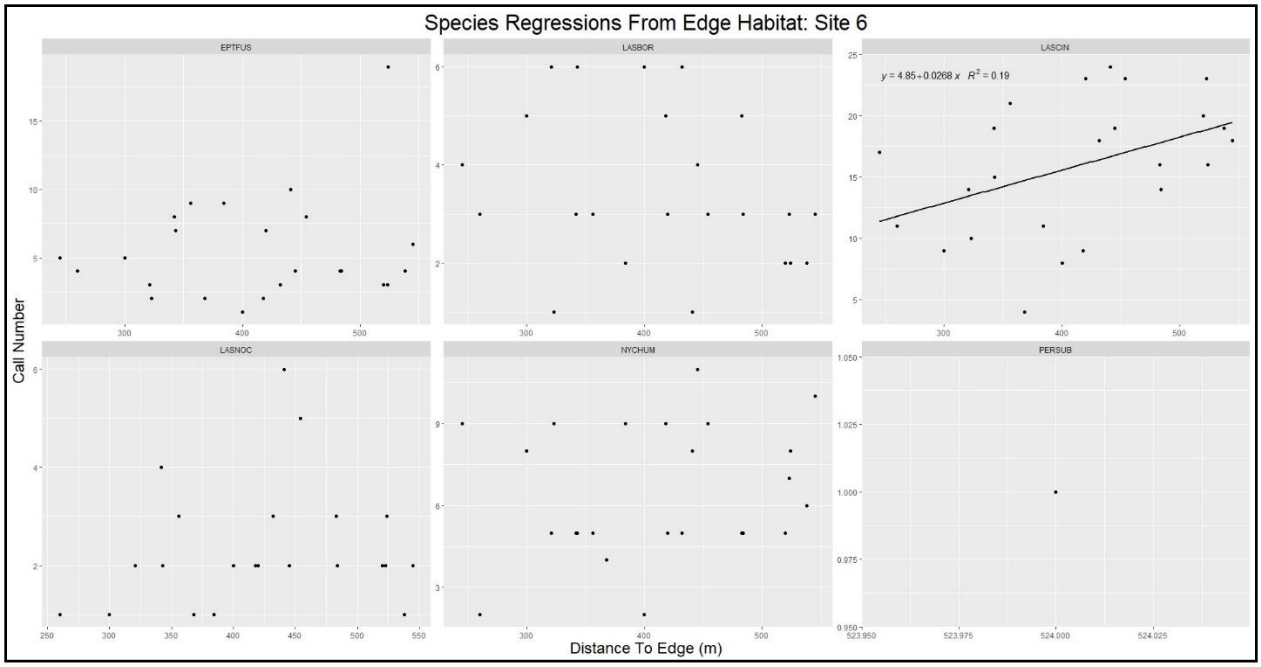


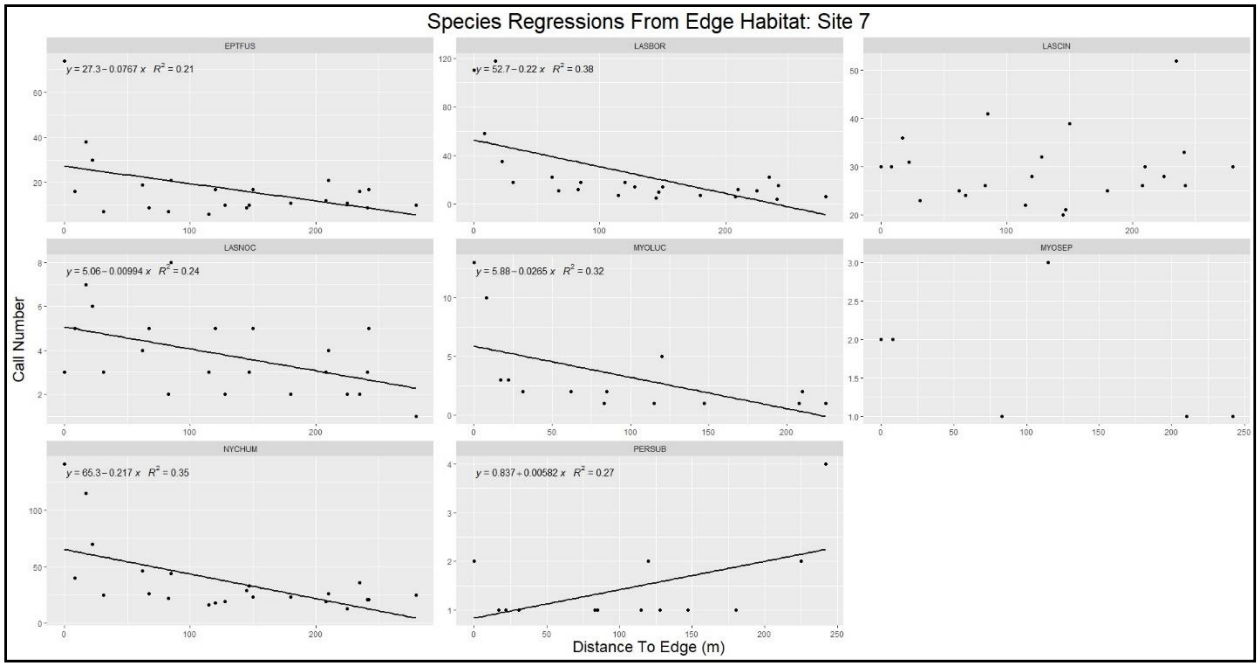

Species Regressions From Edge Habitat: Site 2
EPTFUS
LASBOR
y = 89 − 0.204 x R² = 0.32
LASCIN
LASNOC
MYOSEP
NYCHUM
y = 51.4 − 0.159 x R² = 0.22
Call Number
Distance To Edge (m)

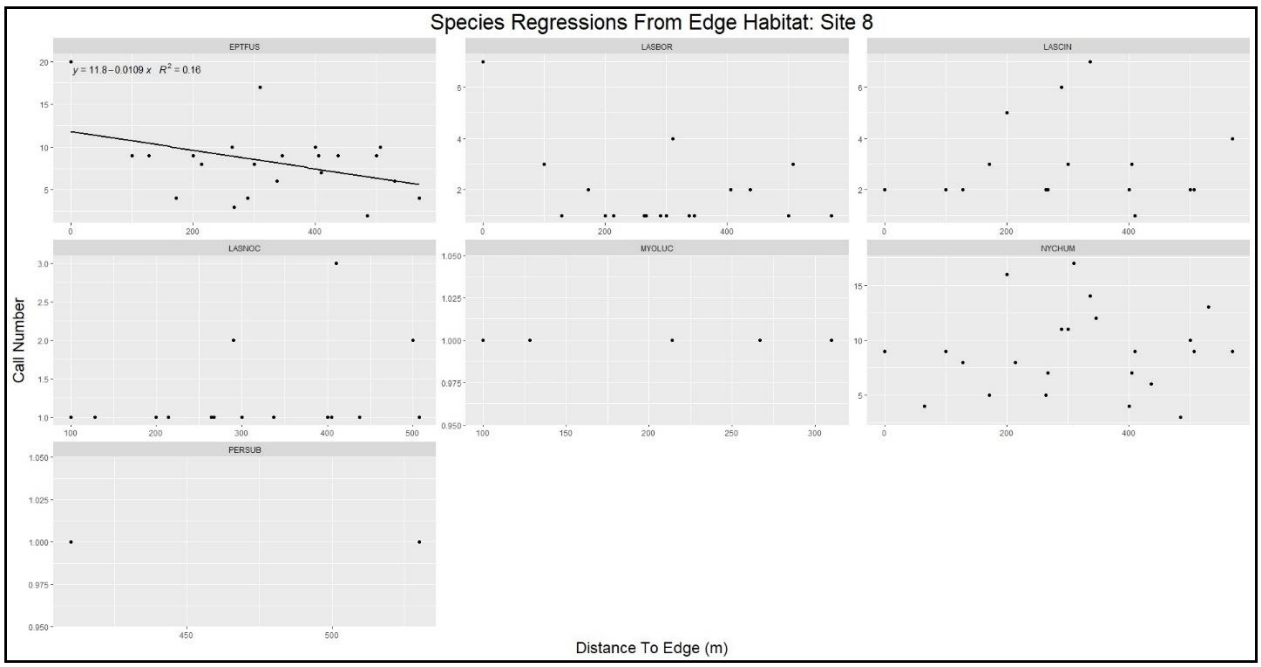

Species Regressions From Edge Habitat: Site 3
EPTFUS
LASBOR
LASCIN
LASNOC
MYOLUC
NYCHUM
Call Number
Distance To Edge (m)

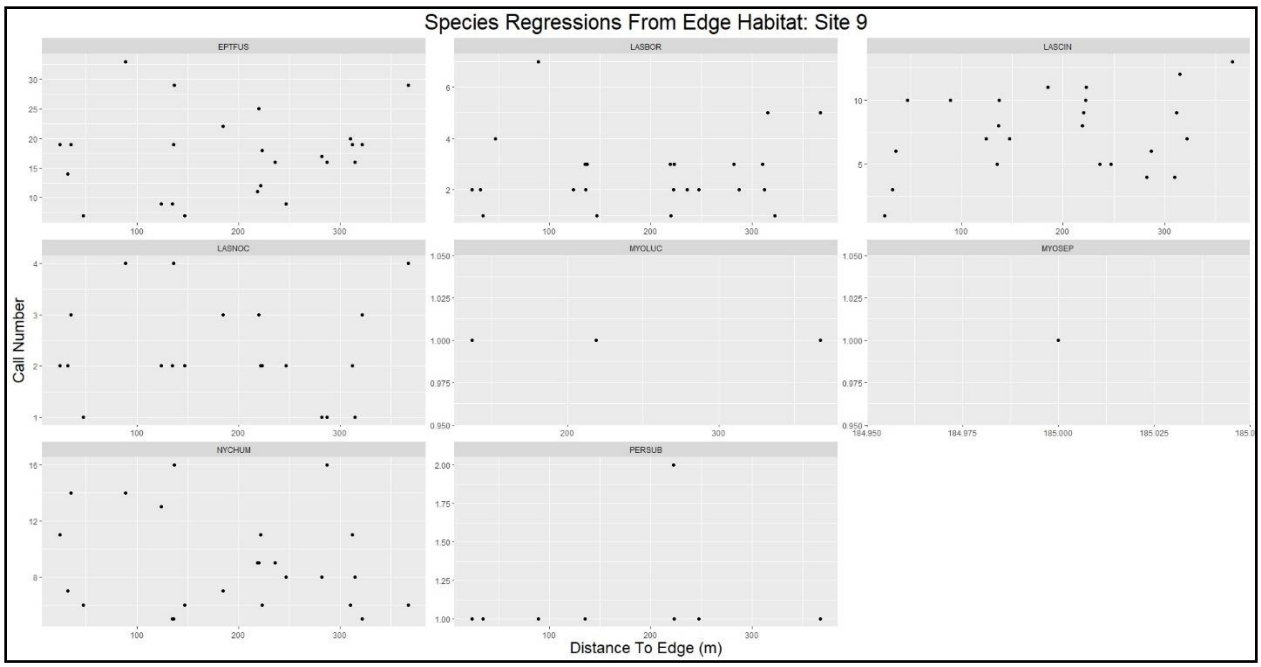

Species Regressions From Edge Habitat: Site 4
EPTFUS
y = 158 − 0.492 x R² = 0.42
LASBOR
y = 32.4 − 0.101 x R² = 0.4
LASCIN
y = 173 − 0.149 x R² = 0.24
LASNOC
y = 19.6 − 0.0372 x R² = 0.39
MYOLUC
NYCHUM
y = 26.3 − 0.0647 x R² = 0.25
PERSUB
Call Number
Distance To Edge (m)

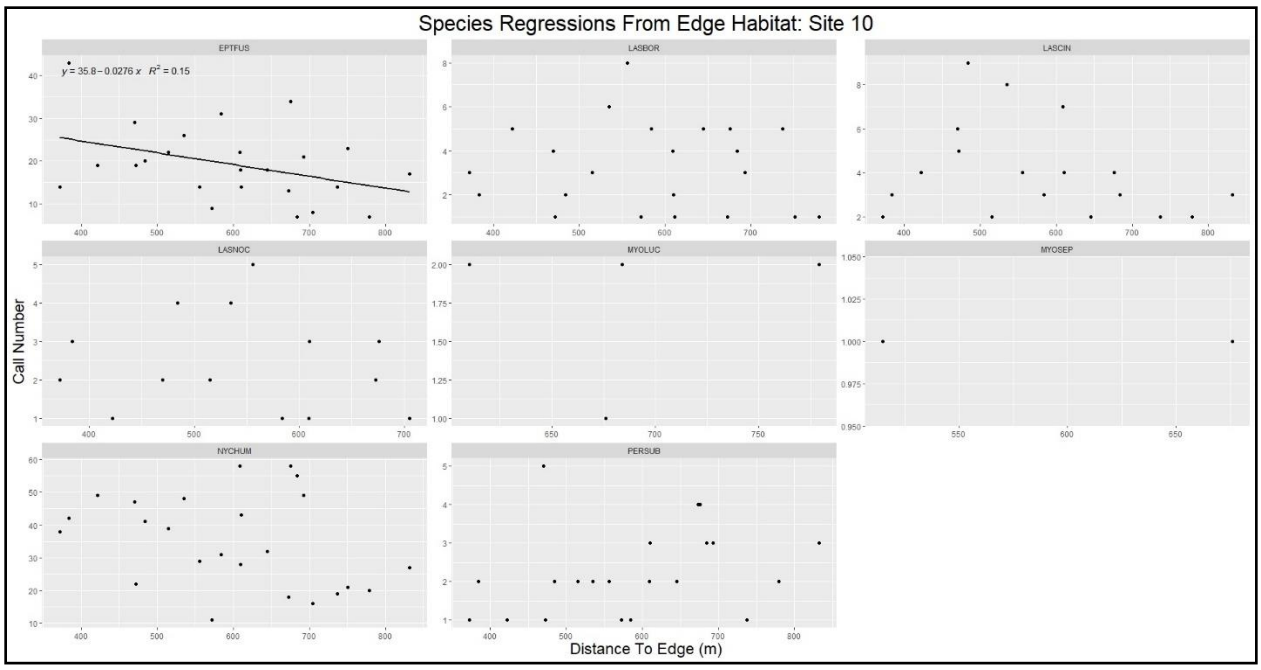

Species Regressions From Edge Habitat: Site 5
EPTFUS
LASBOR
LASCIN
y = 2450 − 8.38 x R² = 0.84
LASNOC
MYOLUC
MYOSEP
NYCHUM
PERSUB
Call Number
Distance To Edge (m)

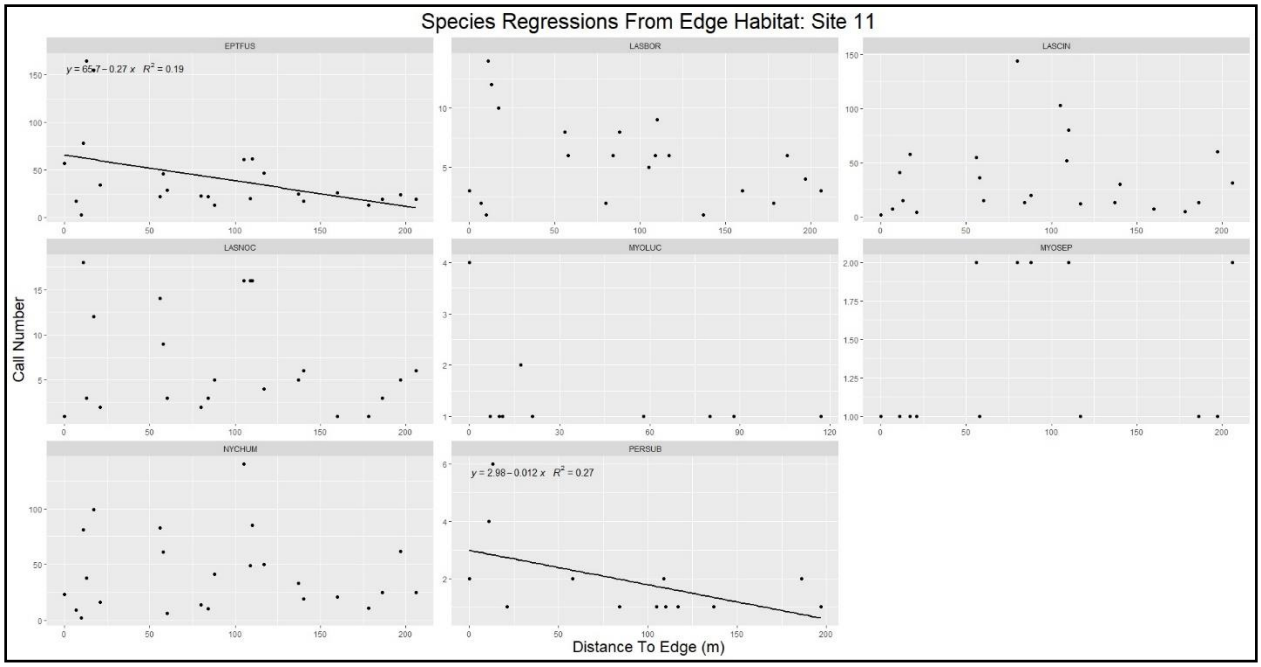

Species Regressions From Edge Habitat: Site 6
EPTFUS
LASBOR
LASCIN
y = 4.85 + 0.0268 x R² = 0.19
LASNOC
NYCHUM
PERSUB
Call Number
Distance To Edge (m)


Species Regressions From Edge Habitat: Site 7
EPTFUS
y = 27.3 − 0.0767 x R² = 0.21
LASBOR
y = 52.7 − 0.22 x R² = 0.38
LASCIN
LASNOC
y = 5.06 − 0.00994 x R² = 0.24
MYOLUC
y = 5.88 − 0.0265 x R² = 0.32
MYOSEP
NYCHUM
y = 65.3 − 0.217 x R² = 0.35
PERSUB
y = 0.837 + 0.00582 x R² = 0.27
Call Number
Distance To Edge (m)

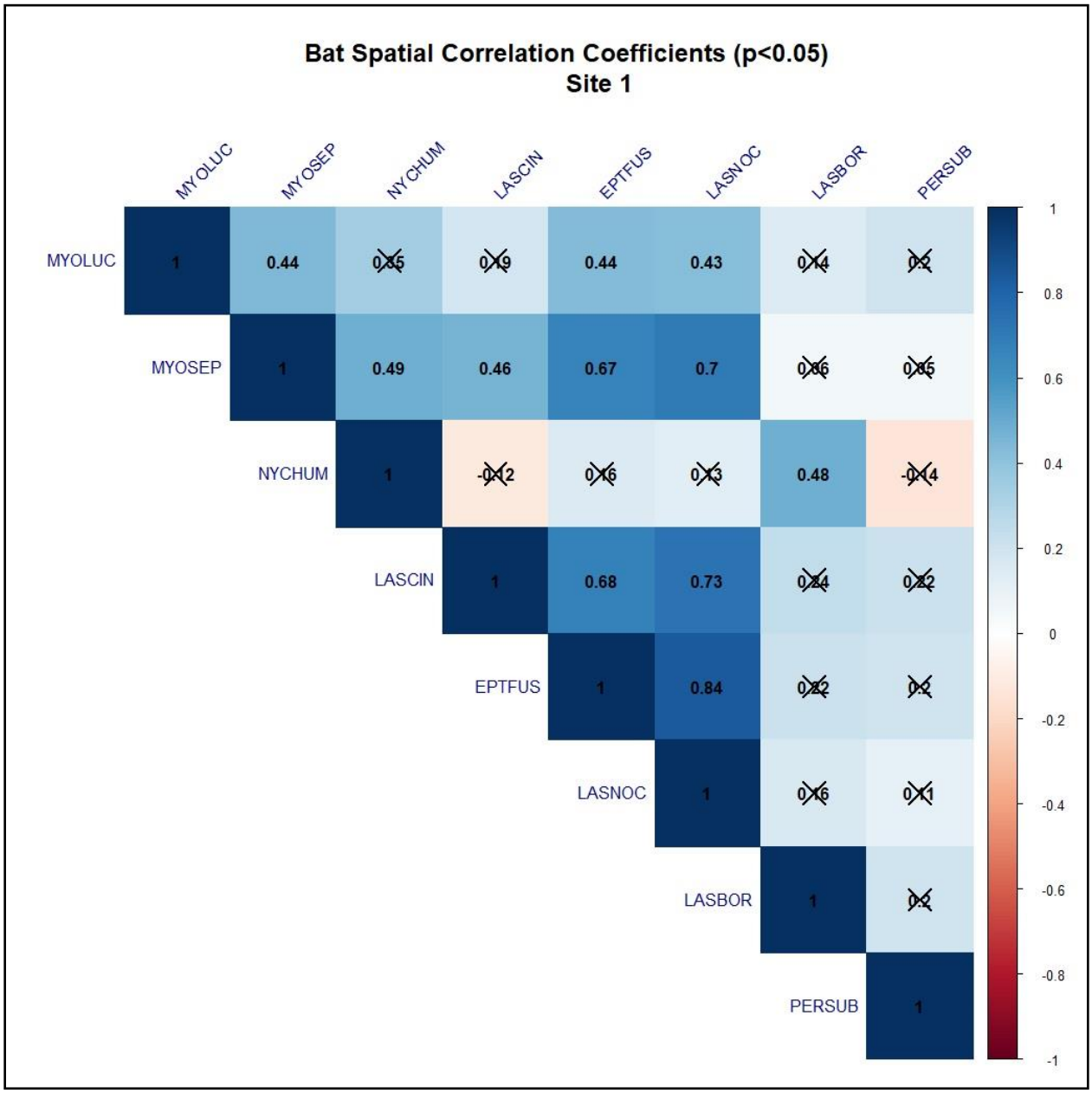

Species Regressions From Edge Habitat: Site 8
EPTFUS
y = 11.8 − 0.0109 x R² = 0.16
LASBOR
LASCIN
LASNOC
MYOLUC
NYCHUM
PERSUB
Call Number
Distance To Edge (m)

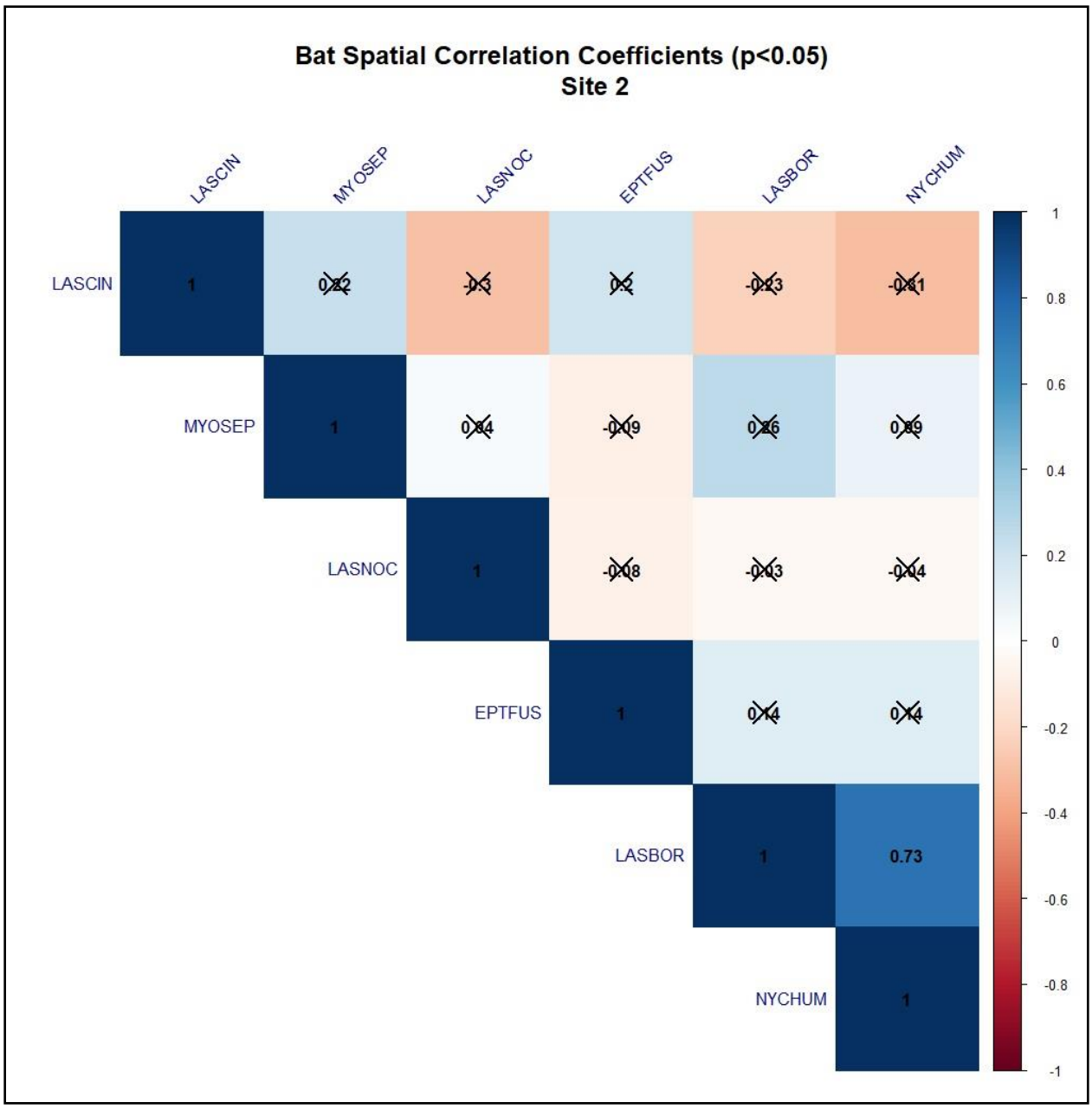

Species Regressions From Edge Habitat: Site 9
EPTFUS
LASBOR
LASCIN
LASNOC
MYOLUC
MYOSEP
NYCHUM
PERSUB
Cali Number
Distance To Edge (m)

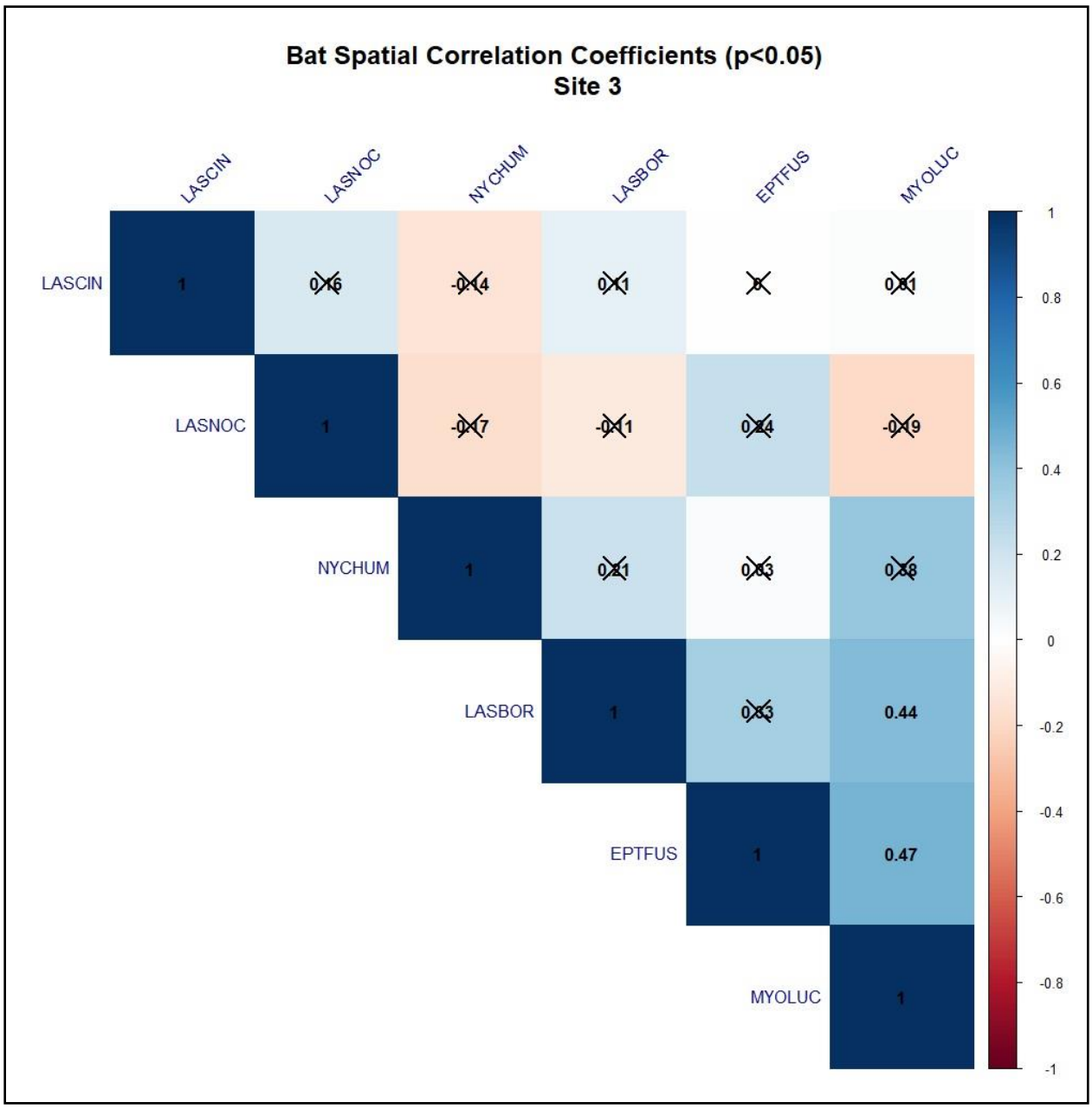

Species Regressions From Edge Habitat: Site 10
EPTFUS
y = 35.8 − 0.0276 x R² = 0.15
LASBOR
LASCIN
LASNOC
MYOLUC
MYOSEP
NYCHUM
PERSUB
Call Number
Distance To Edge (m)

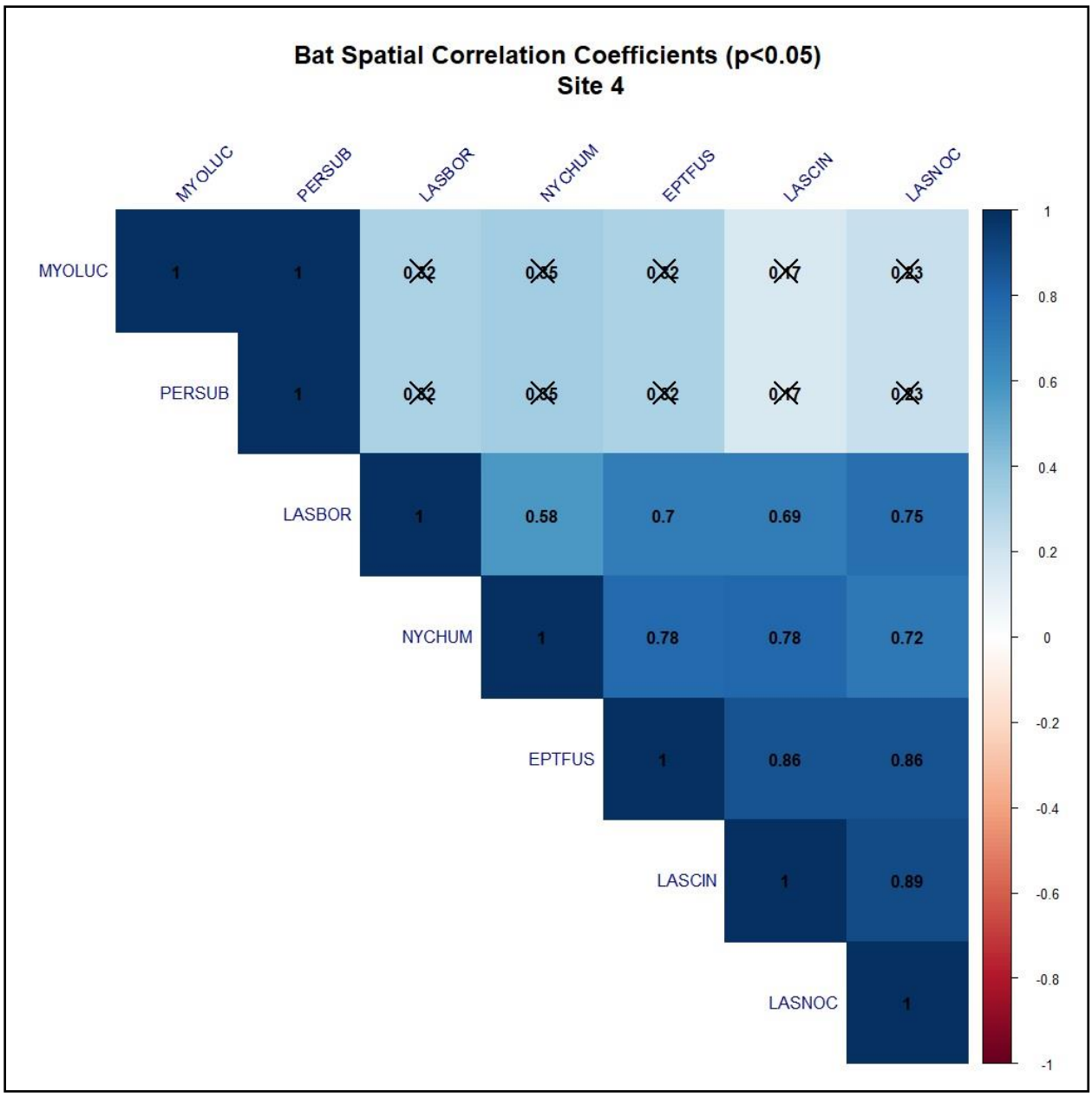

Species Regressions From Edge Habitat: Site 11
EPTFUS
y = 65.7 − 0.27 x R² = 0.19
LASBOR
LASCIN
LASNOC
MYOLUC
MYOSEP
NYCHUM
PERSUB
y = 2.98 − 0.012 x R² = 0.27
Call Number
Distance To Edge (m)

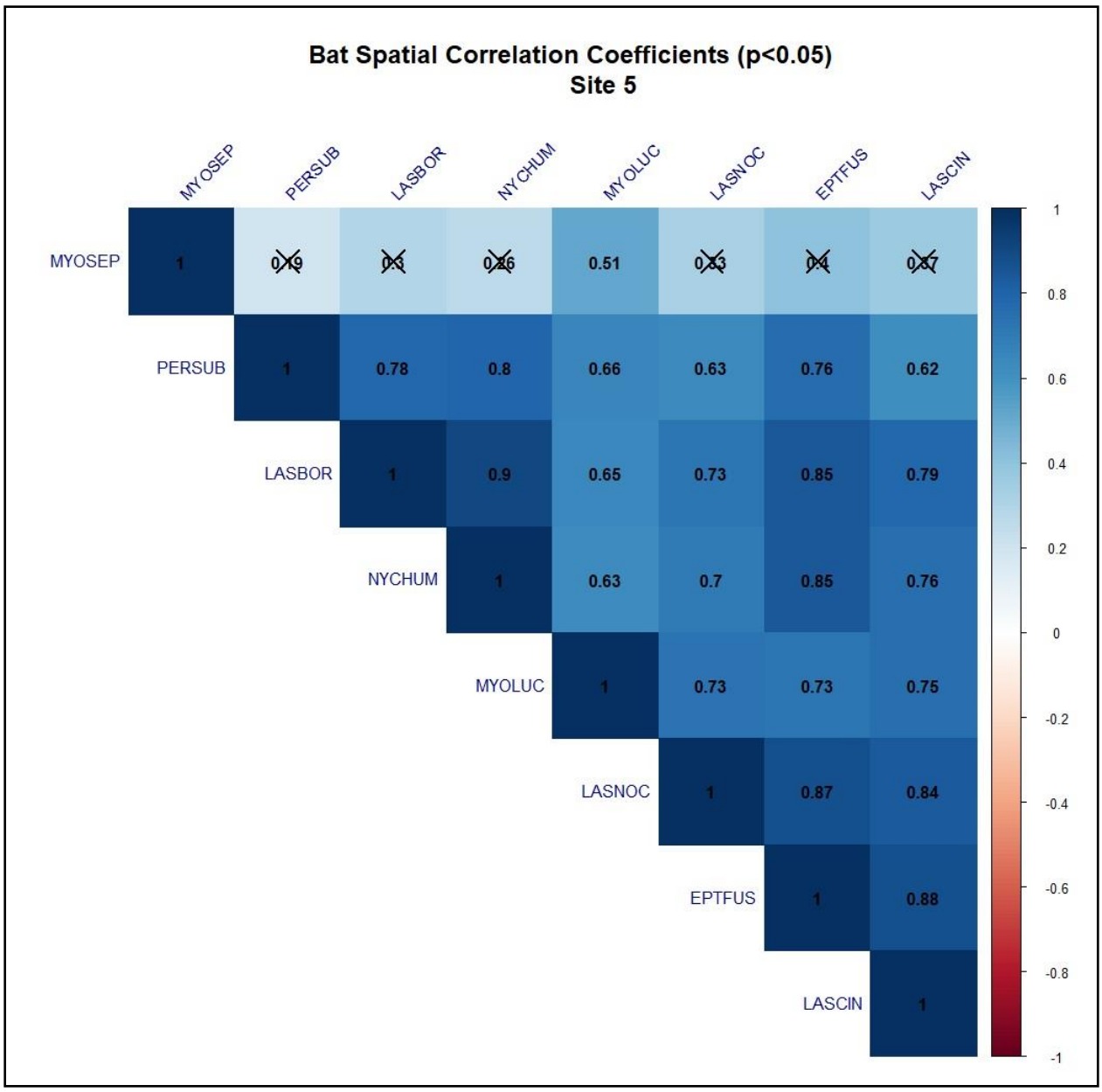
APPENDIX B. SITE SPECIFIC SPATIAL MATRICES OF BAT SPECIES PAIRWISE COMPARISONS FOR STRENGTHS OF SPATIAL CO-OCCURRENCES

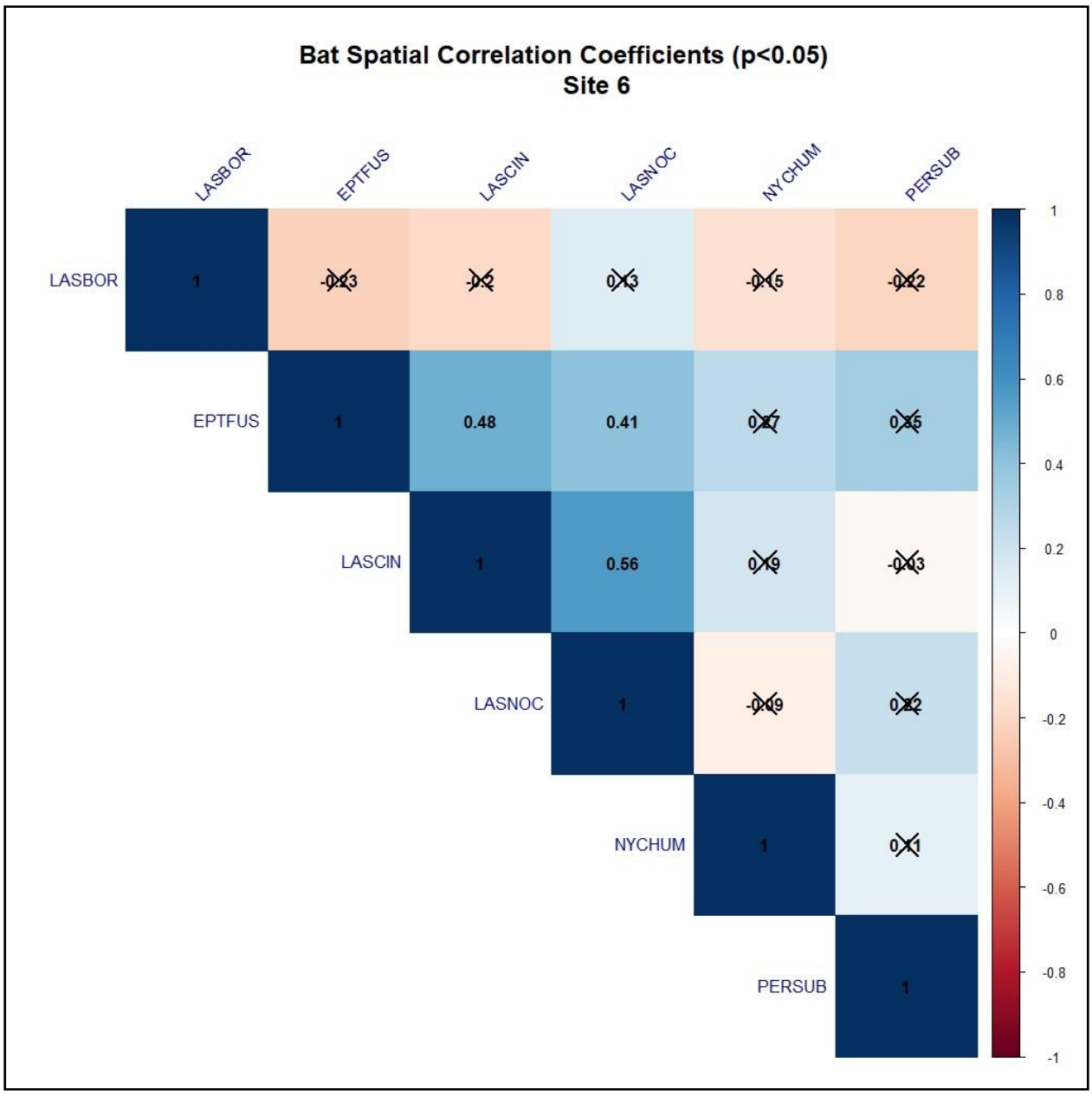


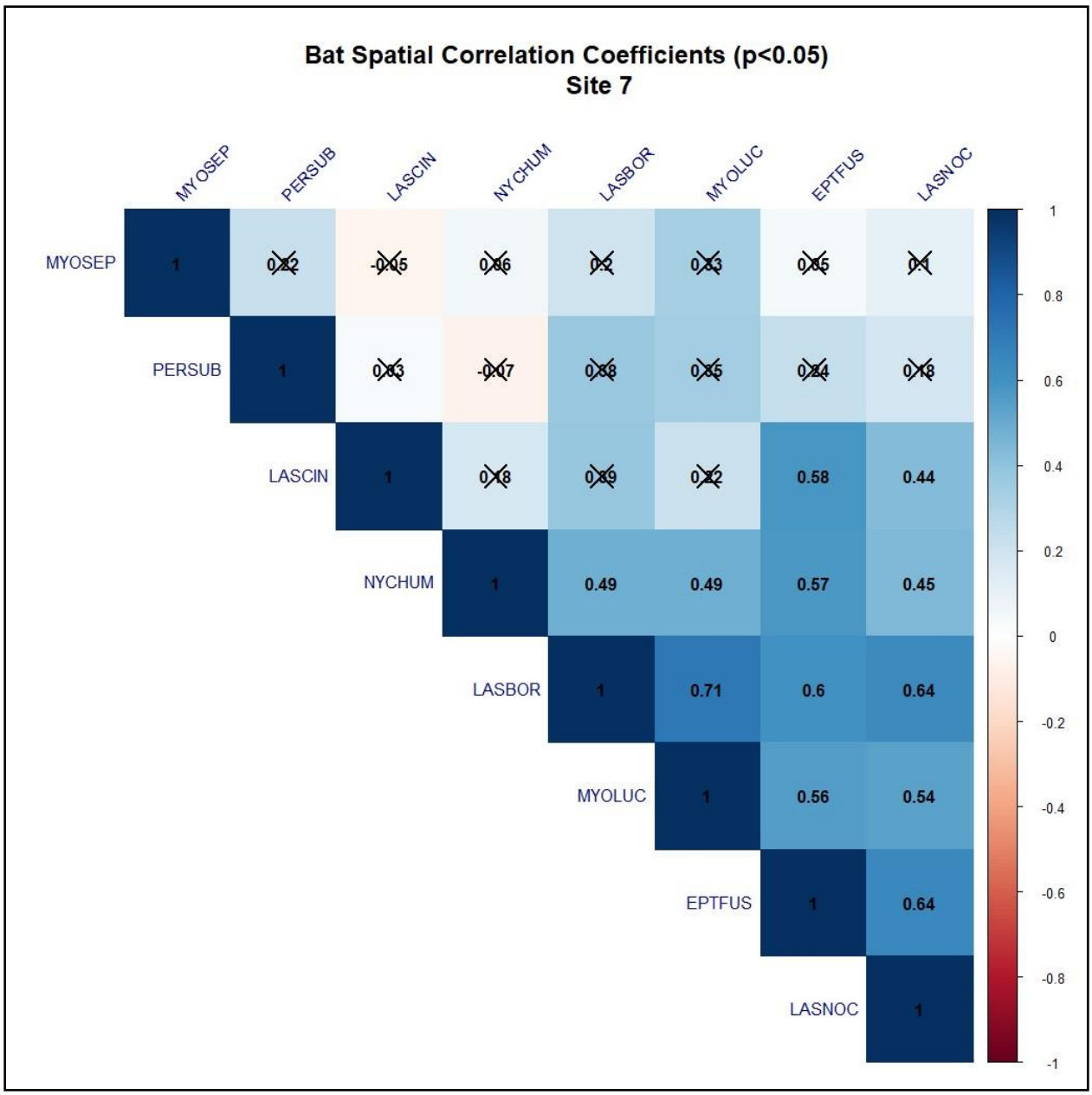

Bat Spatial Correlation Coefficients (p<0.05)
Site 2
LASCIN
MYOSEP
LASNOC
EPTFUS
LASBOR
NYCHUM
1
0.22
-0.3
0.2
-0.13
-0.31
1
0.04
-0.09
0.26
0.09
1
-0.08
-0.03
-0.04
1
0.14
0.14
1
0.73
1
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1

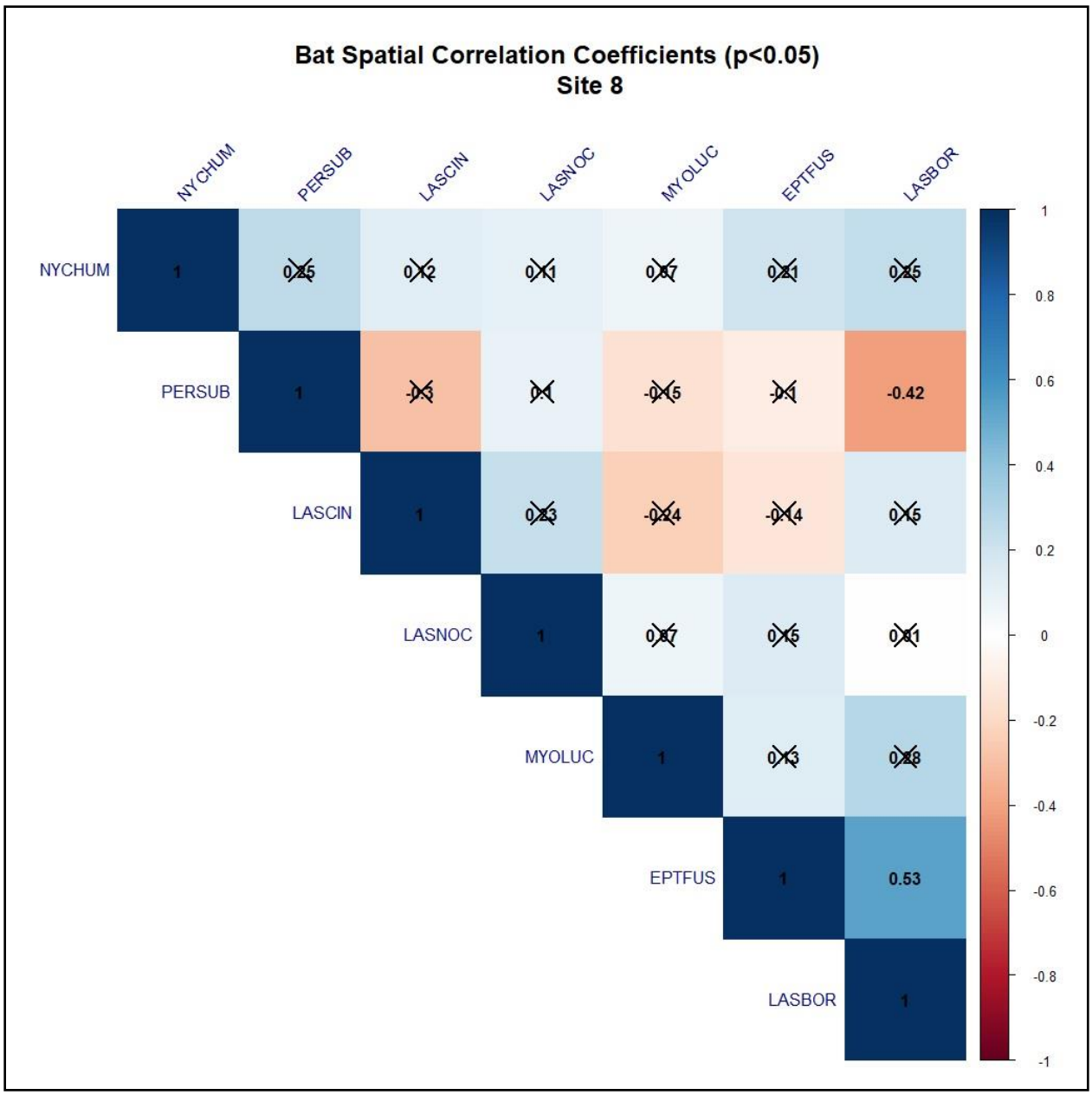

Bat Spatial Correlation Coefficients (p<0.05)
Site 3
LASCIN
LASNOC
NYCHUM
LASBOR
EPTFUS
MYOLUC
1
0.16
-0.14
0.11
0
0.01
1
-0.07
-0.01
0.24
-0.19
1
0.21
0.33
0.38
1
0.33
0.44
1
0.47
1
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1

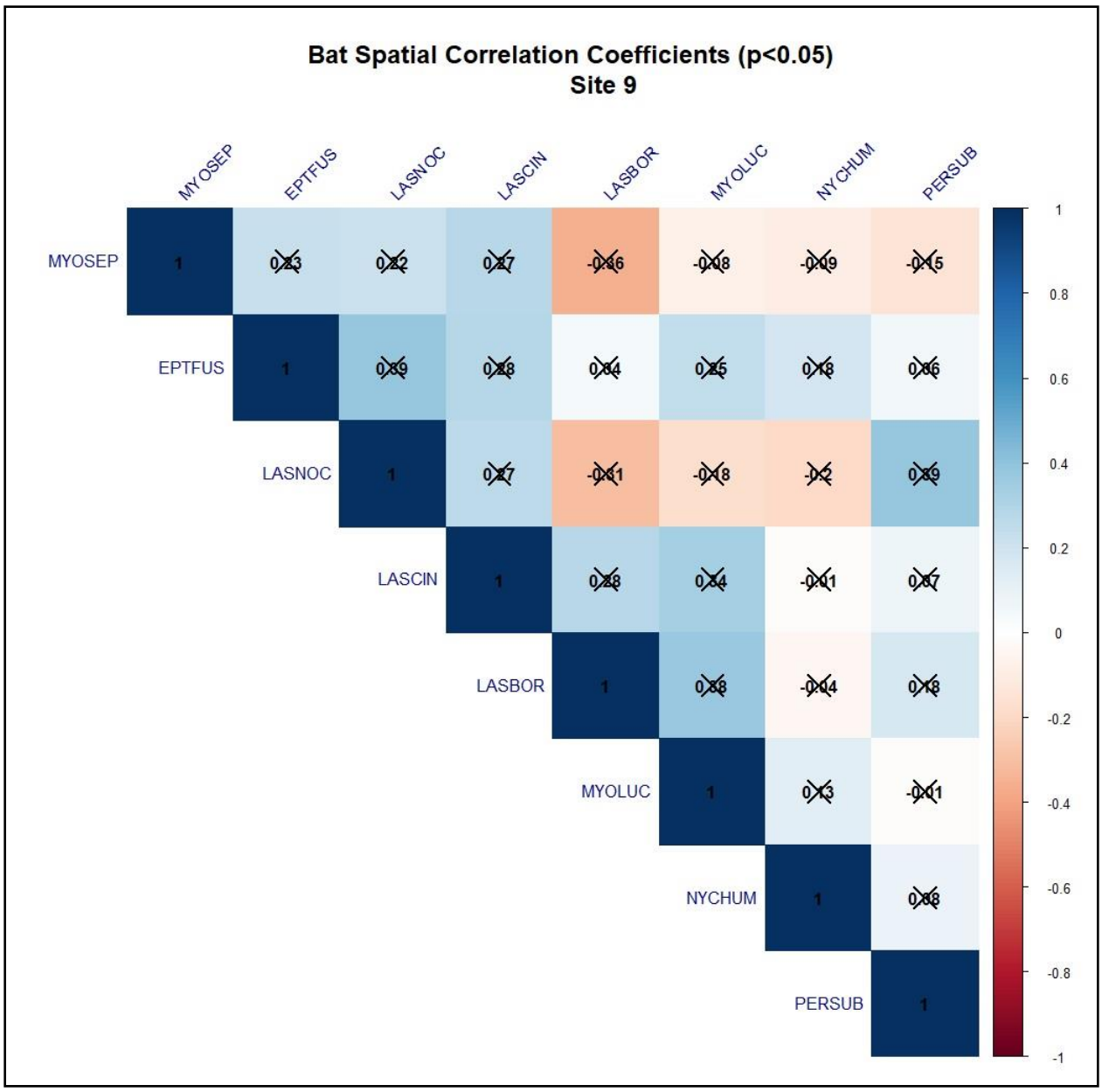

Bat Spatial Correlation Coefficients (p<0.05)
Site 4
MYOLUC
PERSUB
LASBOR
NYCHUM
EPTFUS
LASCIN
LASNOC
1
1
0.52
0.55
0.52
0.47
0.53
1
0.52
0.55
0.52
0.47
0.53
1
0.58
0.7
0.69
0.75
1
0.78
0.78
0.72
1
0.86
0.86
1
0.89
1
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1

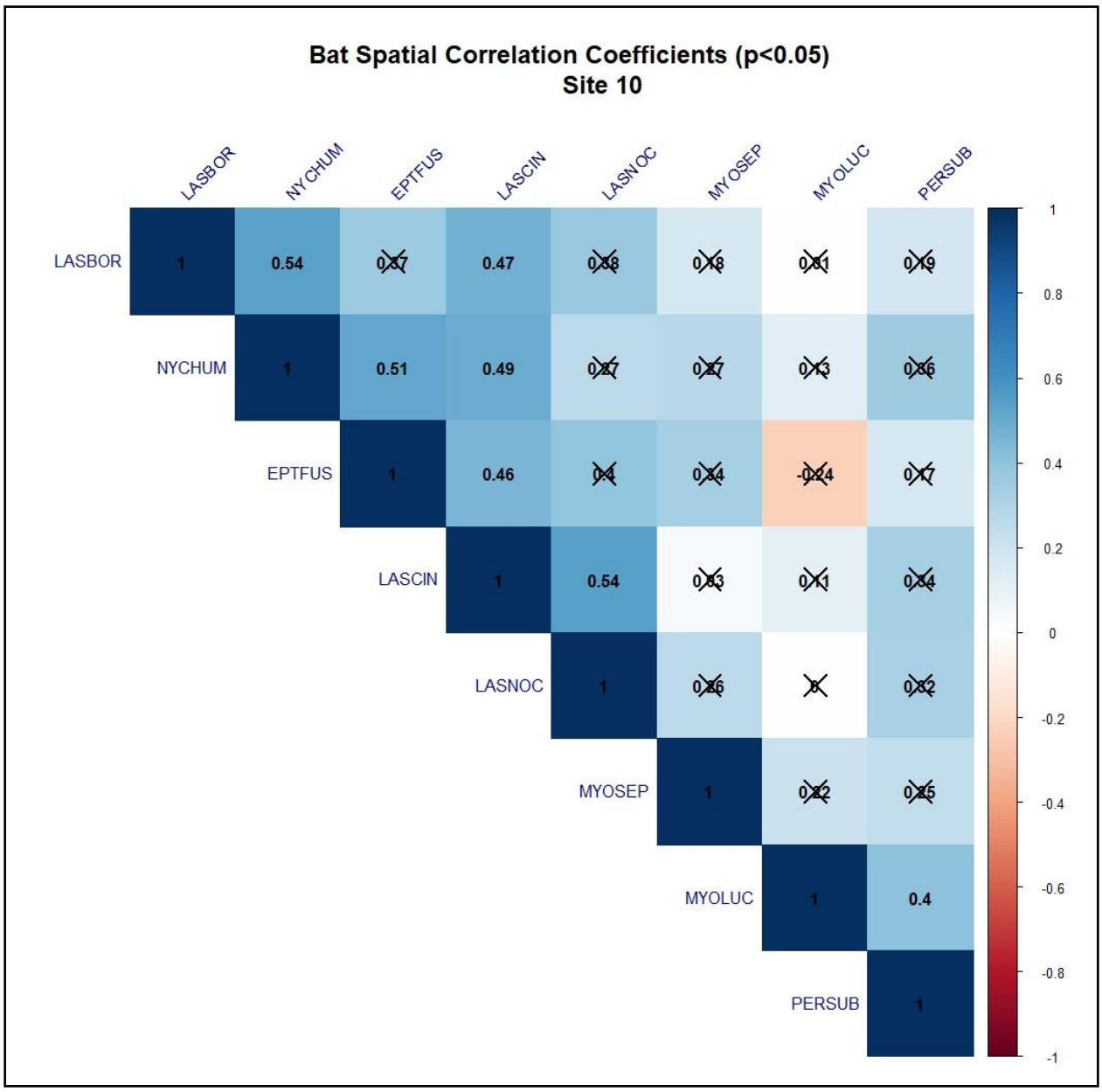

Bat Spatial Correlation Coefficients (p<0.05)
Site 5
MYOSEP
PERSUB
LASBOR
NYCHUM
MYOLUC
LASNOC
EPTFUS
LASCIN
1
0.78
0.8
0.66
0.63
0.76
0.62
0.9
0.65
0.73
0.85
0.79
0.63
0.7
0.85
0.76
0.73
0.73
0.75
0.87
0.84
0.88
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1

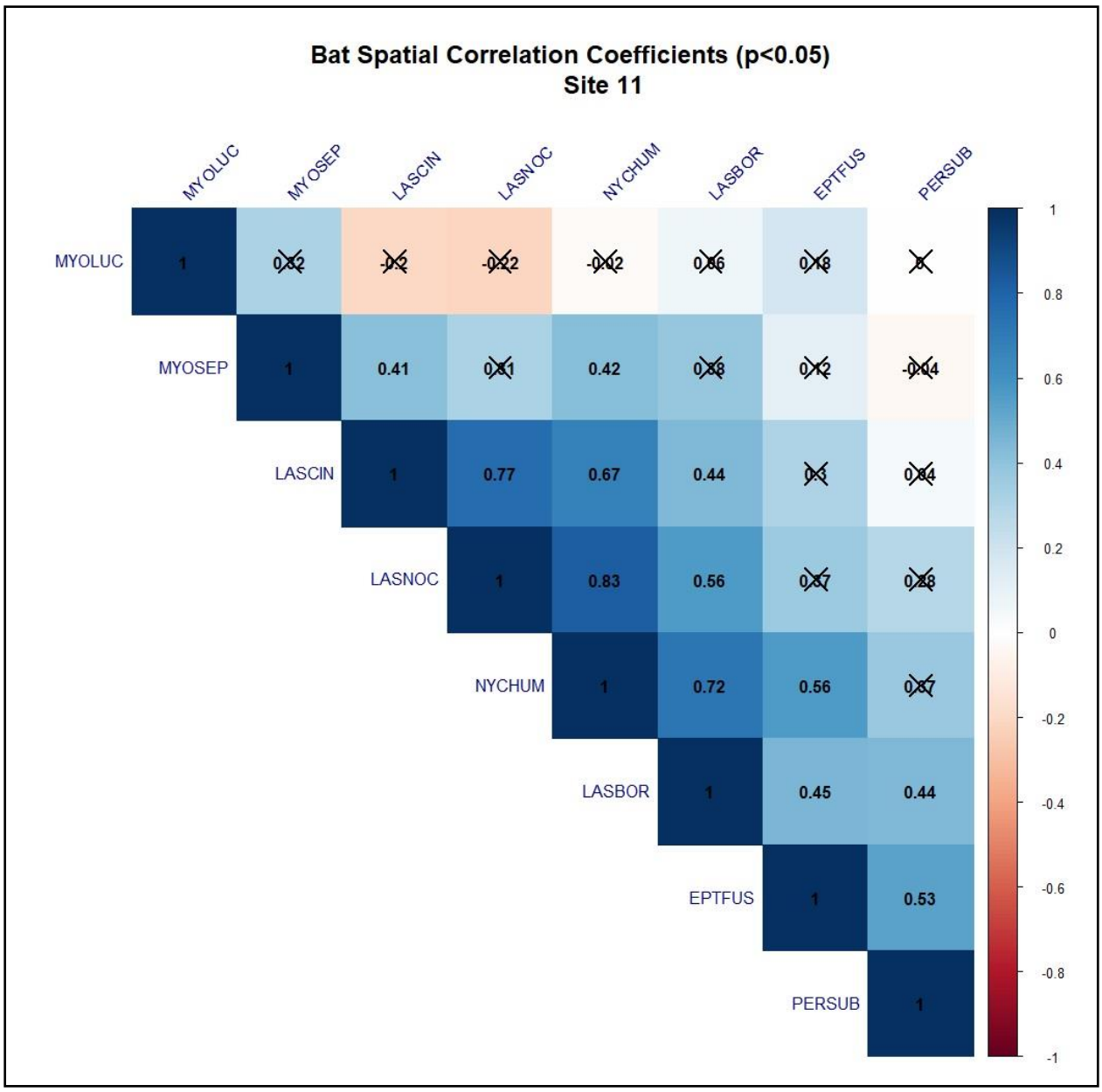

Bat Spatial Correlation Coefficients (p<0.05)
Site 6
LASBOR
EPTFUS
LASCIN
LASNOC
NYCHUM
PERSUB
1
0.48
0.41
0.56
1
1
1
1
1
1
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1

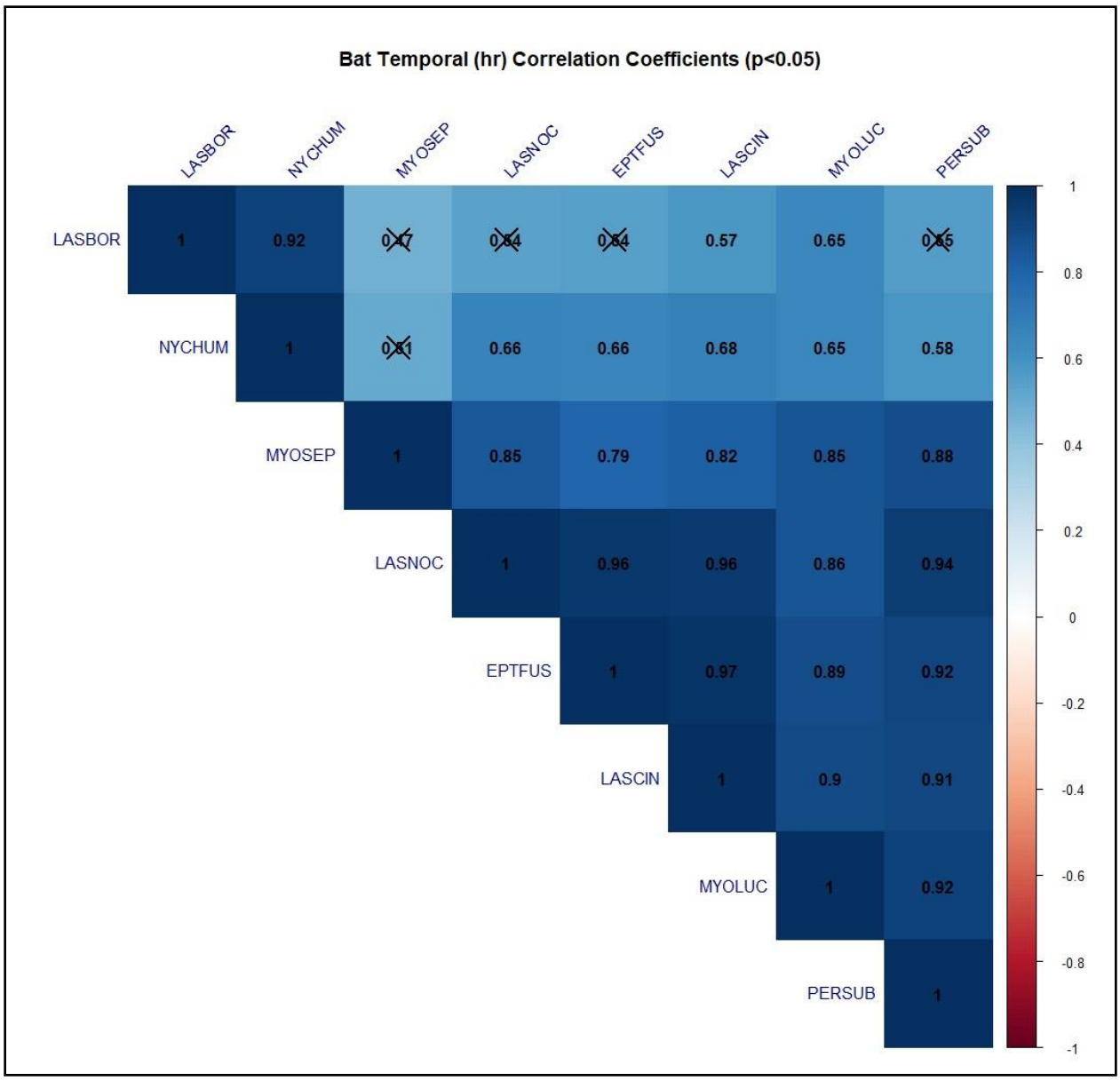

Bat Spatial Correlation Coefficients (p<0.05)
Site 7
MYOSEP
PERSUB
LASCIN
NYCHUM
LASBOR
MYOLUC
EPTFUS
LASNOC
1
0.44
0.58
0.49
0.49
0.57
0.45
1
0.71
0.6
0.64
1
0.56
0.54
1
0.64
1
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1


Bat Spatial Correlation Coefficients (p<0.05)
Site 8
NYCHUM
PERSUB
LASCIN
LASNOC
MYOLUC
EPTFUS
LASBOR
1
0.25
0.12
0.11
0.07
0.21
0.25
1
-0.3
0.1
-0.15
-0.1
-0.42
1
0.23
-0.24
-0.14
0.15
1
0.07
0.15
0.01
1
0.13
0.28
1
0.53
1
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1


Bat Spatial Correlation Coefficients (p<0.05)
Site 9
MYOSEP
EPTFUS
LASNOC
LASCIN
LASBOR
MYOLUC
NYCHUM
PERSUB
1
0.23
0.32
0.37
-0.36
-0.08
-0.09
-0.15
0.89
0.38
0.64
0.25
0.18
0.36
0.27
-0.31
-0.18
-0.2
0.39
0.38
0.64
-0.01
0.37
0.38
-0.04
0.18
0.13
-0.01
0.08
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1


Bat Spatial Correlation Coefficients (p<0.05)
Site 10
LASBOR
NYCHUM
EPTFUS
LASCIN
LASNOC
MYOSEP
MYOLUC
PERSUB
1
0.54
0.47
0.4
0.46
0.54
0.4
1
0.51
0.49
0.4
1
0.46
0.54
1
0.54
1
1
1
1
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1


Bat Spatial Correlation Coefficients (p<0.05)
Site 11
MYOLUC
MYOSEP
LASCIN
LASNOC
NYCHUM
LASBOR
EPTFUS
PERSUB
1
0.41
0.77
0.67
0.44
0.83
0.56
0.72
0.56
0.45
0.44
0.53
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1


Bat Temporal (hr) Correlation Coefficients (p<0.05)
LASBOR
NYCHUM
MYOSEP
LASNOC
EPTFUS
LASCIN
MYOLUC
PERSUB
1
0.92
0.64
0.64
0.57
0.65
0.65
1
0.66
0.66
0.68
0.65
0.58
1
0.85
0.79
0.82
0.85
0.88
1
0.96
0.96
0.86
0.94
1
0.97
0.89
0.92
1
0.9
0.91
1
0.92
1
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1